A COMPARATIVE ANALYSIS OF NESTING LIFE-HISTORY TRAITS AND THE RISK OF PREDATION AMONG ISLAND AND CONTINENTAL BIRDS

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Abstract

Islands are home to one of the most endangered ecosystems today with high extinction rates, deteriorating biodiversity and high numbers of critically threatened species. Part of reason for the current situation is that island biotas are subject to different selective pressures compared to continental environments resulting in differences in life-history traits that may make island species especially susceptible to human-induced changes, especially the introduction of exotic predators. Although earlier studies have found a variety of behavioural and morphological differences between island and continental bird species, few studies have compared the reproductive life-history differences between insular and continental bird species. In this thesis, I compare how island passerines differ from continental passerines in some of their nesting life-histories. I focus my studies on New Zealand birds as this avifauna provides an excellent system to examine the nesting life-history traits of birds on islands that evolved without mammalian predators. At the same time, a large number of continental bird species have been introduced that evolved with mammalian predators, providing an opportunity to compare the two groups in a common environment. First, I compared predation rates of artificial nests baited with the preen waxes of New Zealand endemic birds and compared them to nests baited with continental preen waxes and control nests with no waxes. I expected that the artificial nests of the endemic species would be baited with more volatile ("smellier") preen waxes and thus would depredated at a higher rate. The endemic nests were found to be predated in higher rates than the other nest treatments supporting the 'olfactory crypsis' theory. I then compared behavioural differences in flushing between endemic New Zealand species and continental species. I hypothesised that endemic New Zealand birds which evolved in a predator regime with avian predators but no mammalian predators would behave in ways that increase their vulnerability to mammalian predators compared to continental species. I found that New Zealand birds flushed from nests later or not at all compared to continental species, and returned earlier to the nests after flushing and did not alter their parental behaviours after flushing. All of these behaviours are likely to increase the vulnerability of endemic birds to introduced mammalian predators. Finally, I then took a broader perspective of island life history evolution and assessed evolutionary changes in the nest sizes of insular and continental bird species across a of islands. Island species were found to build larger nests with larger dimensions and overall 'sizes' than their continental relatives. The reasons for the changes in nest sizes may include the higher predation regimes encountered by continental birds, which puts a premium on minimising nest conspicuousness (and thus size). Overall, my findings confirm that life-history traits of island birds differ from those of continental species, and suggest that these differences arise from differences in the intensity of selection from predators. This highlights the unique features of island birds and identifies some of the attributes that may now make them vulnerable to introduced predators.

Chapter 1

1.1 General Introduction

Islands and insular species

Island biology and the evolution of island biotas have intrigued researchers ever since Charles Darwin highlighted the role of islands in the formation of new species. Many of the earliest modern attempts to understand species assemblies (e.g., island biogeography theory [MacArthur and Wilson 1967]) and current theories of community ecology (e.g., meta-community [Leibold et al. 2004]) have their ideas at least partly founded around studies of island biology. This is because islands are small and isolated and provide ideal systems for studying evolutionary processes such as the creation of large radiations of distinct species. The selective pressures that influence plants and animals on islands can be very different from that occurring in continental environments and this can lead to changes in the life-histories of insular species. The objective of this thesis is to uncover some of the differences in life history between insular and continental species of birds.

Many island species around the world have similar evolutionary attributes. The similarities among insular species are assumed to be a result of the different selective pressures experienced in island ecosystems compared that of continents. This leads to the evolution of similar traits among island species through convergent evolution, including larger body size, tameness and lack of flight in birds and insects (Daugherty et al. 1993). The dodo (*Raphus cucullatus*), is a prime example of some of these features. Relatively large-bodied, naïve, and flightless, this bird was hunted to extinction within 50 years of

human settlement after whalers reached the small island of Mauritius. Many other vertebrates including the saddle-backed Mauritius giant tortoise (*Cylindraspis inepta)* quickly followed the dodo's fate over the next 150 years (Cheke and Hume 2008). Island environments differ from continents in various ways including climate, species diversity, intra- and interspecific competition, and trophic level size. Predation risks are also much reduced on islands because distance and lack of dispersal abilities prevented many predators (that are high in the trophic levels) from reaching isolated islands and the lack of food availability often limited their success (Simberloff 1974). Smaller trophic level sizes on islands may ultimately lead to a lack of anti-predatory defences as these behaviours can be costly and no longer functional (Blumstein and Daniel 2005). Islands with reduced predator regimes thus provide important and interesting systems for understanding how different species cope with novel selective pressures such as that arising by predatory mammals.

New Zealand, like many islands, is unique in its evolutionary history, separating from the supercontinent Gondwana early in its geological history, approximately 80 million years ago (Cooper and Millener 1993). Prior to human arrival, the New Zealand terrestrial environment contained few terrestrial mammals with only a few species of small bats. The isolation and lack of predatory mammals lead to the evolution of a distinct fauna with many species of birds being flightless, some insects becoming large and rodent-like and the survival of primitive frogs that disappeared elsewhere. Similarly, New Zealand's diverse endemic flora evolved without mammalian browsing pressure. The lack of mammals led to much of the fauna adopting niches that are typically occupied to mammals on continents. Giant wetas for example, are sometimes referred to as 'invertebrate mice' as

their nocturnal, omnivorous habits and large size share many characteristics that are typically found in small rodents (New 2008).

It is important to note that New Zealand's avifauna, and that of many other isolated oceanic islands, did not evolve in the absence of predators, just the absence of mammalian predators as many islands host a number of avian predators and even some reptilian predators. Species on islands have adapted to generally a much reduced range of predators and the lack of mammalian predators in particular. Avian predators (often the predominant predators on isolated islands) provided ample selective pressures to avoid predation from above with many species of birds becoming nocturnal and showing cryptic colouration in their plumage (Holdaway 1989). Contrastingly, continental environments have predation regimes involving a large suite of predators (mammalian, avian and reptilian). Continental species that co-evolved with a large suite of predators should evolve adaptations against these multiple predators. As many islands around the world originally lacked mammalian predators, the patterns of adaptation seen in New Zealand's biota are repeated elsewhere.

Life history of island species and their vulnerability to extinction

The majority of islands today face pressures that have and continue to degrade island ecosystems, and cause the extinction and decline of insular species. The most important drivers of extinction on islands are species invasions (Vitousek et al. 1996; Vitousek et al. 1997; Sala et al. 2000) and habitat modification (Didham et al. 2005*a*). These drivers often operate synergistically which can exacerbate their impact on island biota (Didham et al. 2005*a*; Didham et al. 2005*b*). Invasive rodents for example, are likely responsible for the greatest number of extinctions and ecosystem changes on islands (Towns et al. 2006;

Howald et al. 2007). The impact of rodents on island ecosystems is so extensive because they are omnivorous (i.e., affecting plants, invertebrates, reptiles, birds and mammals; Towns et al. 2006) and their plastic life-history allows them to spread rapidly. Invasive rodents now occur on over 80% of major islands around the world (Howald et al. 2007). Habitat modification has also greatly affected island ecosystems. Estimates of deforestation rates exceed over 60% on Pacific Islands (Rolett and Diamond 2004). Predictions of bird species extinctions following deforestation on islands often match the current numbers of threatened bird species, indicating that estimates can be made on the extinction debts from once fully-forested islands (Brooks et al. 1997). Furthermore, habitat loss on oceanic islands underestimates extinction rates because invasive species exacerbate extinctions beyond those caused by habitat loss (Brooks et al. 2002). This suggests that islands with high habitat degradation and invasive species can least afford to lose more habitat or else there may be even further extinctions.

Island biotas around the world are generally considered to have been more severely impacted by invasive species and habitat loss than continental biotas (Sala et al. 2000). Island species that persist on small, isolated islands seem to be much more prone to extinction than continental species with their more extensive ranges. Although island species represent a small minority of species worldwide, they dominate the lists of recent species extinctions. For example, since the 1600's, a total of 367 (75%) extinctions involved insular species compared to only 124 species extinctions on continents (Smith et al. 1993). This susceptibility to becoming extinct seems to affect all animal classes with 27% of insular mammals having become extinct since human arrival (Alcover et al. 1998), a purported 2000 species of birds going extinct since pre-human activities (Steadman

1995) and a well documented higher extinction rate for reptiles on islands (Frankham 1998).

Like many other islands, the lack of mammalian predators made New Zealand's unique flora and fauna vulnerable to the impacts of invasive species. The endemic avifauna is especially susceptible to mammalian predators. Species such as the kakapo (*Strigops habroptilus*), a large, flightless and ground nesting bird, possess many life-history traits that increase the risk of predation against ground-searching mammals (Holdaway 1989). The avian predators that were prevalent in New Zealand, hunted using visual cues to locate their prey. However, the mammalian predators introduced into New Zealand rely on olfactory cues to locate prey. As a result, New Zealand's terrestrial avifauna was largely unequipped for the arrival of the predatory mammals introduced by humans. Of the 47 recent extinctions of birds in New Zealand, 61 are of terrestrial origin (Miskelly et al. 2008). This equates to about 40% of the terrestrial avifauna (Daugherty et al. 1993). This high extinction rate was caused by primarily by introduced species such as kiore (*Rattus exulans*), black rat (*R. rattus*), Norway rat (*R. norvegicus*), feral dog (*Canis familularis*), feral pig (*Sus scrofa*), feral cat (*Felis catus*), house mouse (*Mus musculus*), ferret (M*ustela furo*), stoat (*M. erminea*) and weasel (*M. nivalis*; Holdaway 1999). Mclennan et al. (1996) reported that mammalian predation on kiwis were responsible for the failure of 10% of eggs, the depredation of 8% of chicks, 45% of juveniles, and possibly up to as many as 60% of all young birds. This equates to 94% of young kiwi failing to reach adulthood due to predators alone. Competition from introduced species also plays a role in the decline of endemic birds. Introduced *Vespula* wasps for example, compete with endemic birds by reducing the standing crop of honeydew, a key food resource, by about 90% (Beggs 2001). This negatively alters the behaviour of the birds, and may impact their survival and reproductive success. Finally, habitat modification by Maori and European

land clearing reduced forest cover from 82% to 23% (Ewers et al. 2006). The remaining forest cover became fragmented and isolated increasing extinction likelihood of the surviving species. The high extinction rates and various agents of decline emphasises the need to identify the specific attributes of the New Zealand species that make them threatened.

Many endemic New Zealand birds ultimately became extinct because they could not reproduce as quickly as they were succumbing to predation. Reproduction is an essential part of life-history that has been altered (i.e., the success rates) since human colonisation on islands. The avifauna on islands is particularly affected by predators as demonstrated by the marked increase in nest success when predator control is implemented (Coté and Sutherland 1997; Moorhouse et al. 2003; Innes et al. 2010). Mammalian nest predation is thought to have a strong influence on the life history traits of avian species on continents (Slagsvold 1982). Depredation of nests may alter reproductive life history traits such as clutch size, incubation length, nestlings and parental behaviour to increase the probability of nest success. In other words, continental species that have co-evolved with mammalian predators have developed adaptations in their life history traits that minimise their risk of predation. In contrast, insular species evolving in isolation with different (and reduced) predator regimes may have different reproductive strategies that make them more vulnerable to introduced mammalian predators. For instance, New Zealand birds are often large, long lived species with low reproductive rates making them unable to cope with high rates of predation (Daugherty et al. 1993). In this thesis, I examine the differences between the insular and continental birds by examining some life history traits that may have changed on islands that may make them more vulnerable to introduced mammals. I examined three general traits of birds' nesting ecologies. The three traits are: "odour", "flushing behaviour", and "size" of nests.

Outline of thesis

The objective of my thesis is to compare differences between insular and continental birds in a series of traits related to their nesting. The first two data chapters of my thesis (chapters 2 and 3) focus specifically on endemic New Zealand birds by comparing them to continental birds (this includes birds introduced during European colonisation and self-introduced species that evolved on continents). Both chapters focus on the differences in life-history traits between birds on islands and continents: firstly, the odour of birds at their nest and secondly, the flushing response of birds to an approaching potential predator. The third data chapter takes a broader approach by examining changes in nest size on islands around the world.

I start by firstly examining differences in the proneness to nest predation of New Zealand and continental birds that might be due to differences in their odours (chapter 2). Preen waxes are oily substances secreted from the uropygial gland of birds, found just dorsal to the base of the tail (Elder 1954). The waxes are smeared into the plumage as the bird uses its bill to preen. The functions of preen wax in birds are often contentious with theories proposed that include water repellency (Elder 1954), microbial defence (Shawkey et al. 2003), pheremonal activity (Soini et al. 2007) and sexual selection (Zhang et al. 2010). The composition of the preen waxes is also extremely variable with differences found among species (Sweeny et al. 2004), sexes (Jacob et al. 1979) and seasons (Soini et al. 2007). Preen wax chemistry differs in the volatility of the components, with some highly volatile waxes creating strong odours while other, heavier molecular weight components are mostly odourless. Differences in preen wax composition between species should thus create differences in a species' odour ('smell') and this in turn could influence the risk of being detected by a predator that uses olfaction to locate its prey.

Olfactory searching mammalian predators appear to exert strong influences on the composition of preen wax. Reneerkens et al. (2002) proposed the hypothesis that birds experiencing high mammalian predation rates increase their reproductive success with "olfactory crypsis". This postulates that mammalian predators using olfactory cues to find potential prey (both individuals and their nests) should be less able to locate individuals that produce less volatile preen wax. Research has shown that preen wax composition varies in sandpipers, with less volatile diesters secreted during the breeding season, and more volatile monoesters produced in the non-breeding season (Reneerkens et al. 2002). This was further supported by the discovery that olfactory searching mammals have greater difficulty in locating diester waxes than monoesters (Reneerkens et al. 2005) and that the shifts found are only produced in the incubating parents, indicating that it is directly linked to reproduction (Reneerkens et al. 2007). Island species, evolving in the absence of mammalian predators or with limited predation pressures may not produce 'cryptic' preen wax as an adaptation as such a seasonal change would bring no advantages, at least for hiding from predators using olfaction to locate prey. In this chapter, I collected preen waxes from birds that evolved under different predator histories to test whether artificial nests baited with waxes from endemic New Zealand species show increased nest predation rates compared to nests baited with waxes from continental species. If continental birds do have lower nest predation rates compared to endemic New Zealand birds this will support the hypothesis that continental species alter the volatility of their preen waxes to reduce predation at the nest. Similarly, if island species have a higher predation rate, this suggests their nests are particularly vulnerable to mammalian predation because of their increased conspicuousness through their odour.

In the next data chapter (chapter 3), I look at differences in nesting behaviour of forest-dwelling New Zealand passerines and continental birds. High levels of activity around nests may increase the conspicuousness of nests to a predator, and thereby the risk of predation (Martin et al. 2000). Birds experiencing high predation risk often have many adaptations that reduce the probability of the parent and its offspring becoming depredated. Such behaviours include: active parental nest defence, minimising activity around the nest and flushing from the nest when potential predators approach. Flushing behaviours at the nest may involve a trade-off with birds deciding when to flee based upon benefits (potential predator may not locate parent or offspring) and costs (parent or offspring becoming depredated). Nesting birds may have optimal flight strategies in which parents should flee immediately on seeing the predator or only when the predator initiates an attack (Broom and Ruxton 2005). Optimising this trade-off to a point where parents do not flush too early or late at the nest will provide the biggest benefit to reproduction. However, this optimal distance is likely to depend on the predator regime under which a species evolved. For many insular species, fleeing too early may alert an avian predator (i.e., a predator using vision to locate their prey) and it may pay to remain tight on the nest to avoid detection through motion. In contrast, waiting too long in the hope that an incubating individual is not detected visually may make such a bird highly vulnerable to a mammalian predator that can detect the presence by odour alone. In this chapter I test whether the flushing behaviour of native New Zealand birds differs from that of introduced birds.

Insular birds appear to have behaviours and life history traits that make them highly vulnerable to invasive species (Reed 1999). Birds that evolved on islands with low predatory risks sometimes lack anti-predatory behaviours (Blumstein and Daniel 2005). Some anti-predator behaviours may be costly and birds on islands with low predator risks

may lose morphological defences and anti-predatory defences (Blumstein 2002). The nest building behaviours of island species may be constrained in this way as one might expect relatively low selective pressures to retain these behaviours in their 'anti-predator defence repertoire'. I test the hypothesis that the evolutionary history of New Zealand's endemic birds has shaped the nest building behaviours of birds by comparing nest size. Thus, in chapter 4, I conduct a comparative study of nest size differences between island and continental passerines across a large variety of islands. Islands are thought to favour the evolution of a 'medium' body size (Lomolino 1985), longer survival rates and reduced aggressiveness, reproduction, and dispersal (Adler and Levins 1994). These insular life-history changes are explained by a number of environmental differences that occur on islands. These range from founder effects (Clegg et al. 2002) to differences in intra- and interspecific competition, predation rates and resource limitation (Lomolino 2005). The island environments have acted upon insular species for long periods and may cause changes in the pattern of nest construction.

Nest predation is well known to alter the life-histories of many reproductive traits. The smaller clutch sizes in tropical birds for example, are lower, in part due to high predation rates (Snow 1978). Smaller nest size can also be selected by high nest predation rates (Møller 1990). On the other hand, larger nests may be beneficial as they could allow larger clutches to be laid, increase the nesting success by reducing overcrowding and provide more incubation potential for nests. However, the larger the nest, the more conspicuous the nest may be to predators. My study looks specifically at changes in nest size of island species and their continental relatives. This was based across a wide range of islands from small, isolated, oceanic islands to continental 'islands' (formerly connected to

continents). Island species less limited by predation pressures may build larger nests to increase nesting success of their young.

Finally, in the last chapter (chapter 5) I provide a general discussion and highlight the implications of my findings. Island avifaunas have distinct differences compared to continental avifaunas and studying them continues to provide important evolutionary findings. Humans, when they arrived to islands brought about many changes that have degraded island ecosystems. Studying differences between island and continental species will aid in the understanding of the evolution of insular birds and thereby assist in their conservation.

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Chapter 2

Olfactory conspicuousness in island birds: a comparison of predation rates on artificial nests of endemic New Zealand and continental passerines

2.1 Abstract

Nest depredation by olfactory-searching mammals greatly influences the reproductive success of nesting birds. Continental birds have recently been shown to reduce the volatility ("smell") of their uropygial wax (preen wax) during the breeding season to reduce nest predation by mammals using olfactory cues to locate their prey. In contrast, insular birds, such as the avifauna of New Zealand, have had a long evolutionary history without mammalian predators and thus experienced little selective pressure to reduce the wax volatility at the nest. This may make them more vulnerable to predation now that mammalian predators have been introduced. I investigated whether predation rates of artificial nests that were baited with uropygial waxes from either endemic New Zealand birds, or continental birds, or control nests with no wax, differed in risk of predation. I predicted that endemic species would experience a higher risk of predation due to the more volatile nature of their waxes. I found predation rates differed with treatment, with endemic nest treatments depredated at a higher daily rate than the other two treatments. Nests baited with wax from two endemic species (bellbird, *Anthornis melanura*, and South Island Robin, *Petroica a. australis*) had lower daily nest survival rates than any continental species. These results indicate that olfactory crypsis may be reduced in New Zealand birds and this now places them at greater risk of attracting introduced mammalian predators. This higher risk of predation in New Zealand species suggests that island species worldwide may also be at a high risk to nest predation because they are less cryptic in their odour than species that evolved with mammalian predators but this needs to be tested further.

2.2 Introduction

Birds emit various chemical compounds as a part of their normal physiology. These compounds range from the highly volatile, like the sweet and dusty fragrance of the Kakapo (*Strigops habroptilus*; Hagelin and Jones 2007), to less volatile compounds such as some of the high molecular-weight components of uropygial waxes (Jacob et al. 1979). Volatile compounds are widespread in birds, and have been reported in at least 80 different genera, with species in some families (e.g., Procellariiformes, Falconiformes, Psittaciformes, Cuculiformes, Piciformes and Passeriformes) producing waxes that are considered malodorous or uniquely odorous (Weldon and Rappole 1997). Bird odours are produced in a variety of ways. This can be in the form of secretions of the skin such as homobatrachotoxins (Dumbacher et al. 1992), in the excrement (Clark and Woeber 1997), and in environmentally sequestered compounds retained in or on the body such as the oil secretions in the stomach of various Procellariiformes (Clarke and Prince 1976). Much of the volatile chemical compounds (and thus the odour) in birds, however, arises from the uropygial gland, or preen gland (Burger et al. 2004; Soini et al. 2007; Martín-Vivaldi et al. 2010).

The uropygial gland of birds is a mass of fatty tissue embedded beneath the skin and dorsal to the levitator muscle of the tail (Elder 1954). Almost all birds possess an uropygial gland (exceptions include the ostrich), which produces the complex mixture of waxes that by preening is then applied onto the plumage. The preen waxes are comprised of fatty acids and wax alcohols that vary in length and shape (Montalti and Salibián 2000). They consist of lower molecular-mass monoester waxes with carbon number distributions

ranging between C24–C38, to higher molecular-mass diester waxes with carbon numbers in the range of C32–C48 (Sinninghe Damsté et al. 2000). The uropygial gland is extremely variable both in gland size (Galván et al. 2008) and gland secretion composition, with many species of passerines exhibiting variable compounds regardless of phylogenetic relationships, which may possibly infer rapidly evolved differences in function even between closely related species (Sweeny et al. 2004).

The function of preen wax secretions of the uropygial gland is the subject of much debate. Early studies suggested that the uropygial gland may function in the excretion of toxins, including pesticides with the uropygial glands in various birds shown to aid in the excretion of some chlorinated hydrocarbon pesticides (Johnston 1976). Wax secretions may also play a role in water repellency, as branched fatty acids are less water soluble than unbranched acids of the same chain-length, and may therefore be more effective at repelling water and to have a longer retention time on feathers (Sweeny et al. 2004). However, Montalti and Salibián (2000) found no clear relationship between species in uropygial gland size and the degree of exposure to water. The waxes within the uropygial gland impede the growth of bacteria or fungi which can degrade feathers (Shawkey et al. 2003; Galván et al. 2008; Martín-Vivaldi et al. 2009). A study by Moller et al. (2010) suggested that there was a fitness advantage to larger uropygial glands because they are predicted to have less contaminated plumage (more genera of Amblycera chewing lice because larger glands are more effective at killing microbes), and thus their hatching success should suffer less from contamination of the eggs. The study indicated that the uropygial gland functioned in essentially managing the community of microorganisms leading to co-evolution between species. Preen wax secretions may also be used in the sexual selection of certain birds. Female budgerigars (*Melopsittacus undulates*) have a

preference for the male-produced 3-alkanol secretions which synergistically produce a female attractant odour (Zhang et al. 2010). Recently, the olfactory differences between individual bird's preen waxes were suggested to play important roles in parental behaviour at the nest. Incubation lengths of parental birds have been found to reduce temporarily when preen waxes from both hetero- and conspecific birds were applied to their nests (Whittaker et al. 2009).

Whatever the ultimate function of preen wax, its composition is not constant in many species, with changes in the composition of preen waxes both seasonally and between sexes well documented. Seasonal changes in composition of preen waxes have been identified in numerous species of sandpipers (Reneerkens et al. 2007; Reneerkens et al. 2008), plovers (Reneerkens et al. 2006), mallards (*Anus platyrhynchos*; Kolattukudy et al. 1985), dark-eyed juncos (*Junco hyemalis*; Soini et al. 2007), hoopoes (*Upupa epops*; Martín-Vivaldi et al. 2009) and house finches (*Carpodacus mexicana*; Haribal et al. 2005) suggesting similar functions across phylogenies. In domestic ducks, females change the chemical composition of uropygial gland secretions during the reproductive season by producing more diesters (Jacob et al. 1979). This was initially proposed to make the plumage brighter (i.e., through visual discrimination of fit mates) for quality-signalling (Piersma et al. 1999) but diesters are also secreted during incubation (Reneerkens et al. 2002). A recent study by Reneerkens et al. (2007) attributed the differences in wax composition between the sexes to differences in incubation patterns. In sandpipers, diester production differed between incubating and non-incubating species, with diester waxes secreted almost exclusively by the incubating sex in species with uni-parental incubation, and by both sexes in species with bi-parental incubation. Seasonal and sexual changes in

gland secretions could also be mediated by presence of symbiotic bacteria that function to protect eggs against pathogens (Martín-Vivaldi et al. 2009).

Different compositions have Current interest in seasonal changes of preen wax composition has been focused primarily at the underlying changes in reduced volatility of preen waxes for "olfactory crypsis" at the nest (Reneerkens et al. 2002). The change in composition of waxes in many birds results in less volatile waxes, and therefore the reduced conspicuousness to potential predators is the likely reason for switching to diesters during the breeding season. Reneerkens et al. (2005) trained a sniffer dog to locate different amounts of monoester and diester waxes of 14 species of shorebirds. Diester preen waxes were more difficult to locate with the maximum detection distance smaller than monoester waxes, supporting the hypothesis that at least some species of birds change the composition of their preen waxes to reduce the risk that their nest is detected by predators that use olfactory cues to locate their prey. Even if the changes in wax composition also influence symbiotic bacteria (Martín-Vivaldi et al. 2009), seasonal differences in wax volatility will also be subject to selection from predation risk, at least in areas in which predation from predators that use olfaction is severe. There is likely to be high costs involved with diester switching which would actively reduce the likelihood of a species (that evolved in absence of predators) to seasonally switch the composition of their preen waxes. This is supported from Reneerken's et al. (2006) experiment which supplied birds with different daily food limits. Those birds which were food-restricted and only given sufficient food to maintain stable body mass significantly less often switched to diester waxes during the breeding period indicating that there are some energetic costs associated with the shift to diester preen waxes.

Predation of nests by mammalian predators largely determines the reproductive success of many avian species (Skutch 1985; Renton and Salinas-Melgoza 2004). It is not unusual for more than half of all nests to fail due to nest predators. As a result, selection should favour traits that reduce predation on the individual and nest, such as the cryptic colouration and nocturnal habits of the Kakapo (Holdaway 1989), and the cryptic coloration that conceal eggs, nests and incubating birds from visually searching predators (Lee et al. 2010). However, not all predators locate prey by vision, as many nocturnally active mammalian predators rely on olfactory cues to locate prey (Whelan et al. 1994). Waxes from uropygial glands may thus play an important role in providing olfactory crypsis as a potential anti-predation strategy against nocturnal mammalian predators. In other words, preen wax composition is expected to evolve in ways that make it more difficult for olfactory-searching predators to locate.

Birds on isolated oceanic islands that evolved in the absence of predatory mammals, however, may have lacked the necessary selective forces to favour the evolution of olfactory crypsis at the nest. The islands of New Zealand, for example, have been isolated from the Australian continental landmass for the last 80 million years (Cooper and Millener 1993), and lacked any terrestrial predatory mammals until humans arrived and colonised around the 13th century AD (Wilmshurst and Higham 2004). Previous to colonisation there were four endemic avian predators, all of which were birds: laughing owl *(Sceloglaux albifacies*), New Zealand hawk *(Circus eylesi*), Haast's eagle (*Harpagornis moorei*) and New Zealand falcon (*Falco novaeseelandiae*). These avian predators hunted primarily using visual or auditory cues to locate their prey from a distance, and not to "sniff out" their prey at close range as would a predatory mammal. Thus the New Zealand avifauna, with little selective pressures for cryptic olfaction, at least

relative to that experienced by their continental counterparts, may be expected to have lost the anti-predator defences of olfactory crypsis or not evolved them at all. It is possible that the introduction of mammalian predators onto isolated islands such as New Zealand had such an devastating impact because endemic birds with "smelly" preen waxes were easier to detect by potential predators using chemosensory cues. A study of preen waxes in a small selection of native New Zealand birds by Fluen (2008) supported the hypothesis that the preen waxes of island birds are more volatile than of continental species.

In this chapter, I test the olfactory crypsis hypothesis regarding the proposed differences in detectability of the preen waxes between endemic birds of New Zealand, which did not evolve with mammalian predators, and continental birds that co-evolved with native mammalian predators in their native range. I used a series of artificial nest experiments containing eggs baited with preen waxes from either endemic New Zealand birds or from continental species of birds to determine whether predation rates differ between the two groups. Given their differences in evolutionary history, I predicted that nests baited with the preen waxes from endemic species should be subject to higher rates of predation than those baited with preen waxes from continental species.

2.3 Methods

Collection of preen waxes

Preen waxes were collected from a variety of endemic and continental passerines. The waxes were collected from birds breeding in Kowhai Bush, Kaikoura, New Zealand (173°

37’E, 42° 23’S). Kowhai Bush is a 240 ha low-elevation forest primarily consisting of a kanuka (*Kunzea ericoides*) canopy with a dense understory of shrubs. All introduced mammalian predators are present in Kowhai Bush. For a more detailed description of Kowhai Bush refer to Hunt and Gill (1979). The birds were sampled using mist nets and Potter traps with meal worms as bait. The endemic species that were sampled were New Zealand bellbird (*Anthornis melanura*) and South Island robin (*Petroica a. australis*). The continental species sampled were chaffinch (*Fringilla coelebs*), redpoll (*Carduelis flammea*), song thrush (*Turdus philomelos*), blackbird (*T. merula*), dunnock (*Prunella modularis*), yellowhammer (*Emberiza citrinella*) and silvereye (*Zosterops lateralis*). Apart from the silvereye, all the continental species are native to Europe and were introduced to New Zealand in the 19th century. Although they are now in New Zealand, they evolved with predatory mammals (i.e., quolls, and Tasmanian devils; *Sarcophilus harrisii*) in their native ranges and I assumed the composition of their preen wax has not changed since their introduction. The silvereye is classified as a native New Zealand species but only colonised from 1830 onwards (Clegg et al. 2002), so here it is classified as a continental species as it co-evolved in a continental environment and thus would be expected to have similar traits as other continental species.

Preen wax samples were collected from September-January over two field seasons in the austral springs and summers of 2009-10 and 2010-11. These dates coincided with the breeding season of both endemic and continental species. Sexes and age of birds were determined to ensure that preen waxes were sampled only from adult birds. Male birds were deemed to be in breeding condition by the identification of an enlarged cloacal protuberance when examined in the hand. Females and incubating males were identified by the presence of a brood patch. Birds caught with small cloacal protuberance or no brood

patch were sampled but as I was unsure of their maturity and breeding status they were consequently not used in the analysis. Birds that were recaptured were not reused to ensure that each sample was independent.

The samples of preen wax were extracted from the birds by gently massaging the papilla of the uropygial gland (figure 2.1). Massaging the uropygial gland led to a secretion of a small droplet of wax that was then wiped onto small circular pieces of filter paper. All birds when sampled were massaged with tweezers covered with a film of candle wax; the wax coating was applied to avoid injuring the bird and was burnt off and replaced between individuals to avoid contamination. To ensure an adequate sample, and to standardise the amount of preen that was collected, each bird's papilla was massaged a series of five times. Each time the extruded wax was absorbed onto the same circle of filter paper. Filter papers circles were 3 mm in diameter and cut to identical size using a hole punch. In each case, the collected wax was absorbed across the entire surface of the filter paper. This ensured that a constant surface area of preen wax was exposed to a potential predator as it was not possible to ensure the total volume of preen wax collected was the same across individuals. The filter papers were stored out of the sunlight in coded airtight plastic containers and then were stored in a -19°C freezer until enough samples were collected to conduct an artificial nest experiment (see below). The waxes were stored for no longer than 3 months at a time.

Wax eggs and artificial nests

Wax eggs were made out of blocks of wax using an egg-shaped mould. The mould was used to control for egg size ensuring all eggs were exactly the same size. The eggs all

weighed ~7 g each and averaged 2.8 mm long by 2.1 mm wide. Eggs were similar in size to those of the larger species of passerines (e.g., song thrush, bellbird) which they were intended to mimic. Stainless steel pins were used to pin the filter paper circles containing the preen wax samples onto the wax eggs. Each egg was fitted with either a filter paper circle containing papers baited with preen wax from an endemic New Zealand species, or a continental species, or with no wax (i.e., clean filter paper). Two eggs of the same type were placed into each artificial "nest." I did not construct nests to avoid the confounding effects of odours from nesting materials and instead simply placed the two eggs in a shallow depression similar to that used by many ground nesting species of non-passerine birds. Nests were placed in a grid formation, with the grid consisting of parallel lines 50 m apart and stations marked at 50 m intervals along each line. The grid was contained entirely within the forested areas of Kowhai Bush. A particular nest treatment (i.e., endemic, continental, no wax) was randomised within the grid regardless of treatment. Nest sites were 50 m from the nearest other nest.

Recording procedure

Nests in the grids were checked every two days and eggs examined for signs of predation. The fine grain of the wax used readily recorded marks made by teeth of predators. Rubber gloves were worn whenever eggs were handled to ensure that my scent was minimised as olfactory-searching predators can cue on human odours left around artificial nests (Whelan et al. 1994). A nest was considered to have been preyed upon when at least one of the two wax eggs had been removed or partially eaten. I considered each nest to be an independent observation. Any remains of predated nests were removed and no other nests were put into that position to avoid pseudoreplication. The nests were followed for six days in total and

then removed. A total of 140 nests were tested with 35 endemic wax baits, 35 no wax baits and 70 continental wax baits used.

Statistical analysis

I compared predation rates between the three treatments in two ways. Firstly, a chi-square analysis was performed on the proportional difference in number of nests predated for each treatment. The analyses compared the predation rates between treatments (endemic/island birds; continental/birds from continents; control/no wax) and species used within the treatments. Secondly, the daily probability of nest survival during the experiment was calculated for each treatment and species using the Mayfield method (Mayfield 1961; Mayfield 1975). This provided an estimate of daily nest survival which was then used to calculate an estimated rate of survival over the incubation period based on the average incubation periods for all the birds in this study (Bosque and Bosque 1995). Estimates of variance for each survival probability were calculated using the method in Hensler and Nichols (1981). The software package CONTRAST (Hines and Sauer 2007) was used to compare survival probabilities between species and treatments. The statistical tests were performed on the data under a critical value of $p = 0.05$. Note that not all birds were used in some analyses due to small sample sizes.

2.4 Results

The daily probabilities of nest survival for the three treatments after two and six days of exposure are shown in table 2.1. Amongst the three treatments there was a significant difference in the daily nest survival probabilities after 2 days ($X^2 = 183$, df = 2, $p < 0.001$) and after 6 days exposure ($X^2 = 133$, df = 2, $p < 0.001$). The endemic treatment had significantly lower probabilities of nest survival than the continental or control treatments. Nest survival probabilities extrapolated through an incubation period of 14 days was also significantly different between treatments when using survival estimates from six days ($X^2 = 2003$, df = 2, $p < 0.001$). When species were analysed separately, there was a significant difference in survival probability rates between species (table 2.2; $X^2 = 6115$, df = 4, $p < 0.001$). The three continental species were significantly less likely to be depredated than nests of the two endemic species (table 2.2; $X^2 = 1456$, df = 1, $p < 0.001$). Both of the endemic species studied (bellbirds and South Island robins) were more likely to become depredated than any other species (Figure 2.3).

2.5 Discussion

I found that artificial nests baited with the preen waxes of endemic New Zealand birds were more likely to become depredated, with lower daily nest survival rates compared to nests treated with continental bird's preen waxes or control nests with no preen waxes. The nests of the two endemic birds (bellbirds and South Island robins) were depredated earlier

in the experiment and more often than any nests of the other species. In contrast, nests treated with the preen waxes of the continental birds were often depredated later and less frequently. Nevertheless, my results should be treated with caution and viewed as preliminary as there was a limited sample size and it was difficult to control other confounding factors, such as wax longevity and sex of the bird from which the wax was collected. Despite these problems, there were significant differences in predation risk between artificial nests of endemic birds and continental birds, suggesting that olfactory crypsis is either absent or less well developed in New Zealand birds, and thus is a topic that warrants further research.

The olfactory crypsis theory proposed by Reneerkens et al. (2002) is based on the assumption that a reduction in the volatility of preen waxes will reduce the potential for predators that rely on olfaction for foraging, to locate nests. It has been suggested that this may be the underlying the reason why continental birds switch to diester preen waxes during incubation in the breeding season, as diesters are less volatile than monoesters which should reduce the ability of a predator to locate the odour of a nest. However, it is unclear how much preen wax is retained in the nest by incubating parents and whether the wax could be used as a cue by a searching predator. As birds spend many hours at the nest during incubation, and make direct contact with the eggs and nest while they incubate, they likely make the nest rich with their preen waxes. This is likely to be supplemented by preen waxes remaining on old feathers, dead skin cells, etc., in the nest itself. As mammalian predators have been shown to differ in their ability to locate different preen waxes (Reneerkens et al. 2005), birds subject to high predation pressures from mammals at the nest should be under strong selective pressures to produce more cryptic (i.e., less volatile) waxes in the breeding season. Fluen (2008) showed that shifts to less volatile

secretions in the breeding season have been consistently found among continental birds. In contrast, island birds, which evolved in isolation from predatory mammals, did not lessen the volatility of their waxes (and occasionally produced even more volatile secretions) in the breeding season. This suggests that changes in the composition of preen waxes is linked to changes in predation pressures with endemic island birds having been under less selective pressures to evolve olfactory crypsis due to a lack of predators using olfaction to locate their prey.

I found that nests of the endemic birds were more severely depredated than in the other two nest treatments. The daily nest survival rates and the overall incubation survival rates of the endemic nest treatments were lower than both the continental nests and no wax treatments. Although the nests of the endemic birds were significantly more depredated than both other treatments, the no wax nests were also depredated in high numbers. This suggests that although there was a difference in numbers of nests depredated, other factors are likely to play a role, and a larger sample size is required to fully evaluate the effects of preen wax composition of nest predation risk. Nevertheless, my results support previous studies that suggest continental species reduce the volatility of their preen waxes as an adaptation to increased predation risk from mammals (Reneerkens et al. 2007; Fluen, 2008). Island birds are subject to different selective pressures (low predator numbers, resource limitation, high competition) than continental birds, which can effect various aspects of their life histories, including morphology (Clegg et al. 2002), reproduction (Griffith 2000) and behaviour (Blumstein et al. 2006). These environmental differences may reduce the likelihood for evolving preen wax that has reduced volatility. Non- volatile diester waxes for example, are known to have higher molecular weights and may be more energetically costly to secrete (Reneerkens et al. 2006). As island populations are highly

competitive intraspecific interactions and often limited in resources, it may be maladaptive to reduce the volatility of waxes. Thus the differences between islands and continental environments make it unsurprising that island birds seem to differ in preen wax properties.

This lack of switching preen waxes during the breeding season does not bode well for endemic New Zealand birds, and perhaps other island endemics around the world, as my results suggest that they will be vulnerable during the breeding season to nest depredation from olfactory searching predators. Olfactory searching predators may be able to locate nests of island species with greater ease because of their greater smell than the nests of other introduced continental passerines. Nest predation has had major effects on the evolution of birds with nest predation affecting reproductive attributes such as clutch size, and the length of the incubation period (Yanes and Suárez 1997) and nest size (Moller 1990). Island birds traditionally evolved with low levels of nest predation, but the sudden increase in predation risk due to introduced mammalian predators makes them particularly susceptible to population declines as many island birds are considered "K" selected and have low reproductive rates and longer life spans than their counterparts on continental areas. Extinctions of island birds are known to occur as a direct result from predation at the nest (Savidge 1987). Smellier nests may be one a reason for the high threatened status of many island endemics in the world today.

Predation rates were found to vary among species with endemic bellbirds and South Island robins experiencing much higher predation rates than any other species. Silvereyes, even though they are considered a native species in New Zealand, had higher survival rates than the two endemic species. This is not surprising given that silvereyes are of continental origin, having self-naturalised in New Zealand only during the 19th century, so their recent arrival would likely limit any wax composition changes due to

local selective pressures in the last century. Fluen (2008) found that even a few thousand years of divergence from continental species may be too short of a period to change wax volatility. New Zealand fantails (*Rhipidura fuliginosa*), which are congeneric to their Australian cousins (*R. albiscapa*; Nyári, et al. 2009) still retain "continental-type" preen waxes as they shift to less volatile secretions in the breeding season. It was also reported in Fluen's (2008) study that South Island robins secrete waxes in complete contrast to the "olfactory crypsis" hypothesis by producing more volatile secretions in the breeding season. I found a slight, although insignificant difference in the predation rate between bellbird and robin nests (14 day survival rate of 49% and 44%, respectively) as might be expected with South Island robins producing more volatile preen waxes. It is also possible that both species contain large amounts of volatiles and so both are equally attractive to a predator.

Although I found evidence indicating a difference in predation risk between the artificial nests tested, there were a number of confounding factors that potentially affected my analysis. The first is the longevity of preen waxes in the field. There has been little research into the persistence in preen waxes when exposed to environmental conditions and it is possible that most of the highly volatile components are soon lost. Thus, I could not be sure that enough preen wax remained after the 6 days of my experiment to even be detected by a potential predator. However, some highly volatile waxes of woodhoopoes (*Phoeniculus purpureus*) frequently remain detectable to even humans for long periods after handling the birds (Burger et al. 2004). Similarly, kakapo feathers still retain a strong smell years after collection (J. Briskie, pers. comm.). It is not known how long the preen waxes remained detectable to olfactory-searching mammals in this study but it is likely to be persistent for at least a couple of days and requires further research. The sex of the individual that the preen wax was taken from may also have altered the risk of predation in

this study. Reneerkens et al. (2007) showed that volatile preen wax shifts depend on the incubation patterns (both sexes incubate; only females incubate or only males incubate). During the breeding period, diester preen waxes was secreted almost exclusively by the incubating sex suggesting that diester waxes have a function that is directly related to incubation. This experiment, due to limited resources used both female (47%) and male (53%) preen waxes even though only two of the nine species used are biparental incubators (in all other species the incubating parents are females). Nevertheless, recent research has shown that this may not hold true for all birds with both sexes of South Island robins switching to a similar degree (Fluen 2008). Phylogeny is also a major issue when it comes to my analyses. The endemic island birds used in this study were more closely related to each other than any of the continental birds meaning that the results of this study may be the result of one evolutionary event. Further studies controlling for phylogeny could rectify this.

Although preliminary, my findings do support the olfactory crypsis hypothesis and present an insight into future productive avenues of research on preen wax. Clearly, the next step in this field would be to conduct more in depth and broad scale comparisons of preen wax chemistries of incubating birds, their eggs, and their nests, from species of different origins (island/continental) to determine whether island endemic bird nests are indeed a large "smelly" target for olfactory searching predators. Secondly, it would also be interesting to perform studies on island species with different mammalian predator histories (islands with naturally low numbers of mammalian predators compared to offshore islands with no predator histories). This would help determine if changes in wax chemistry are the result of constraints set by mammalian predators rather that other island

effects such as limitations in the energetic costs of producing diesters that are imposed by greater resource limitation and higher competition in island environments.

These results ultimately suggest that the more volatile waxes of island species may be yet another life-history trait that has lead to island species adapting poorly to the presence of introduced predatory mammals. In the Pacific region alone it has been estimated that 2000 species of birds may have been lost predominantly through predation from introduced mammals and deforestation (Steadman 1995). New Zealand has lost more than 40% of all terrestrial bird fauna (Holdaway 1989) and has the largest percentage of threatened bird species in the world (over 40% threatened; Hilton-Taylor 2000). This contrasts with the success of introduced and self-introduced species in New Zealand with five European passerines (chaffinch, blackbird, song thrush, dunnock and redpoll) and the self-introduced silvereye, accounting for over 30% of all bird individuals (Diamond and Veitch 1981). The dissimilarity in success of the two groups of species occurs partly from the difference in vulnerability to mammalian predators. The absence of island endemics switching to less volatile preen waxes during the breeding season may make island nests smellier and highly vulnerable to mammalian predation compared to continental species. In addition to other aspects of their life-histories (i.e., morphology, reproduction and behaviour) the plight of New Zealand birds may be so perilous because they are also smellier.

2.6 References

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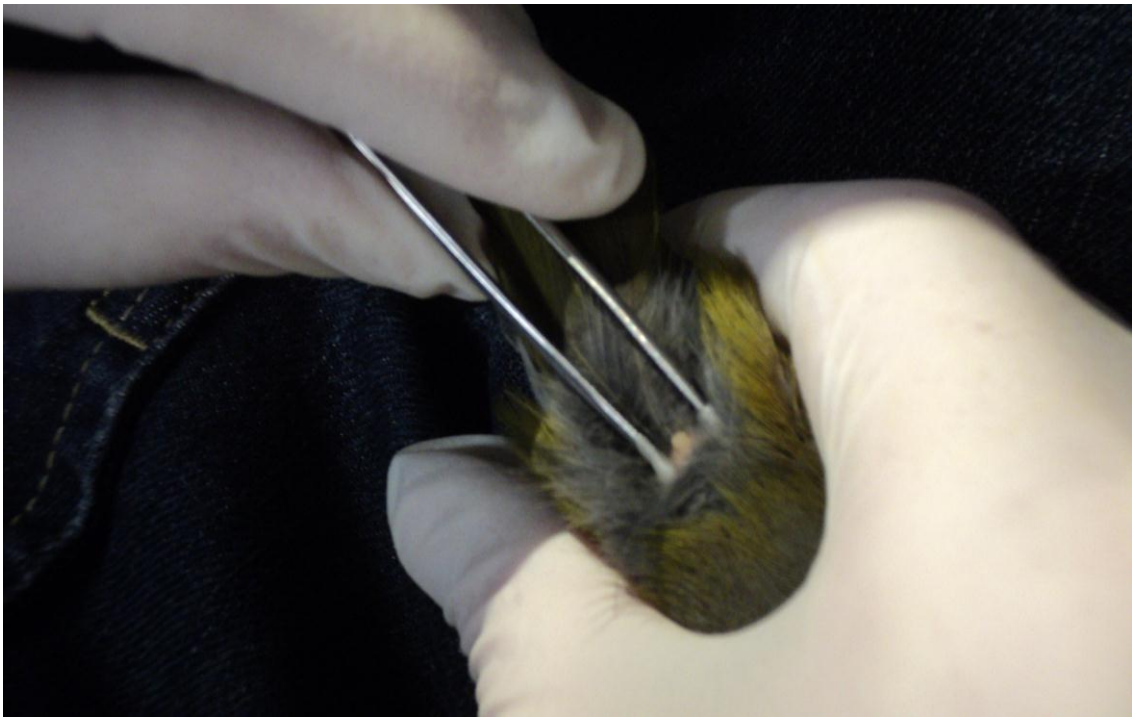

Figure 2.1. Preen wax sampling method from the uropygial gland of a silvereye (*Zosterops lateralis*).

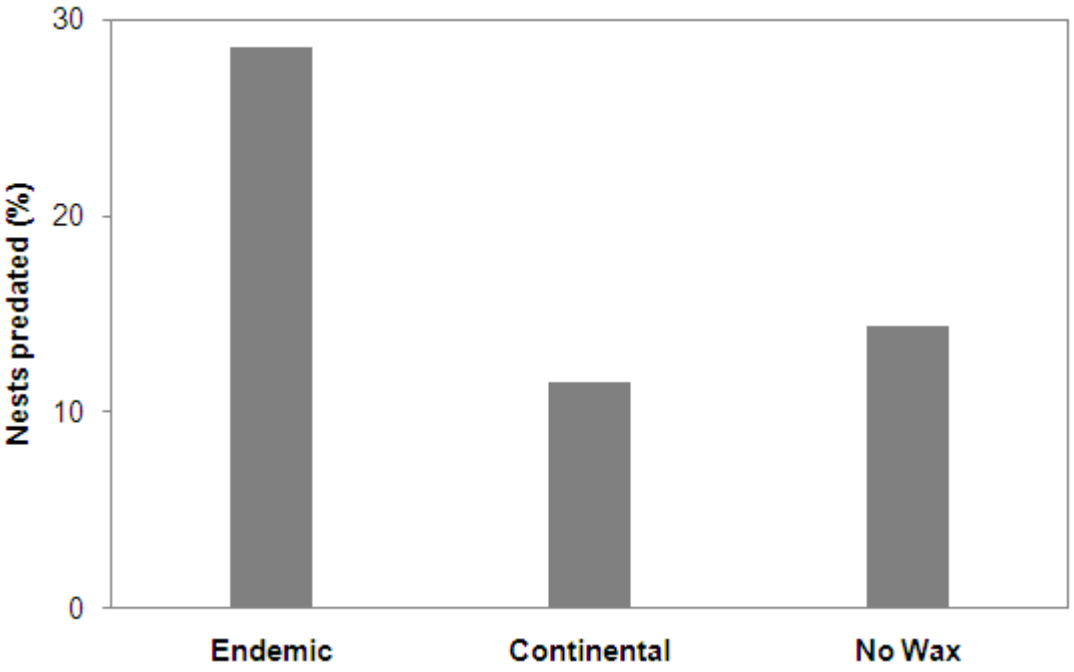

Figure 2.2. The difference in the percentage of artificial nests predated after six days for each nest treatment.

Table 2.1. Daily percentage of nest survival after two and six days for each nest treatment and the predicted incubation period survival from the six day daily nest survival rate. Sample sizes are given in parentheses.

Treatments	**Daily nest survival**		**Incubation period survival**
	Two days	**Six days**	**Six days**
Endemic (35)	95.7	94.7	46.9
Continental (70)	100.0	98.0	76.4
No wax (35)	97.1	97.5	69.9

Table 2.2. Daily percentage of nest survival after two and six days for each species and the predicted incubation period survival from the six day daily nest survival rate. Sample sizes are given in parentheses.

Treatments		**Daily nest survival**		**Incubation period survival**
		Two Days	**Six Days**	**Six Days**
Endemic				
Bellbird	(22)	95.5	95.0	48.8
Robin	(13)	96.2	94.3	43.9
Continental				
Silvereye	(35)	100.0	98.0	76.4
Chaffinch	(13)	100.0	98.7	83.4
Redpoll	(8)	100.0	100.0	100.0

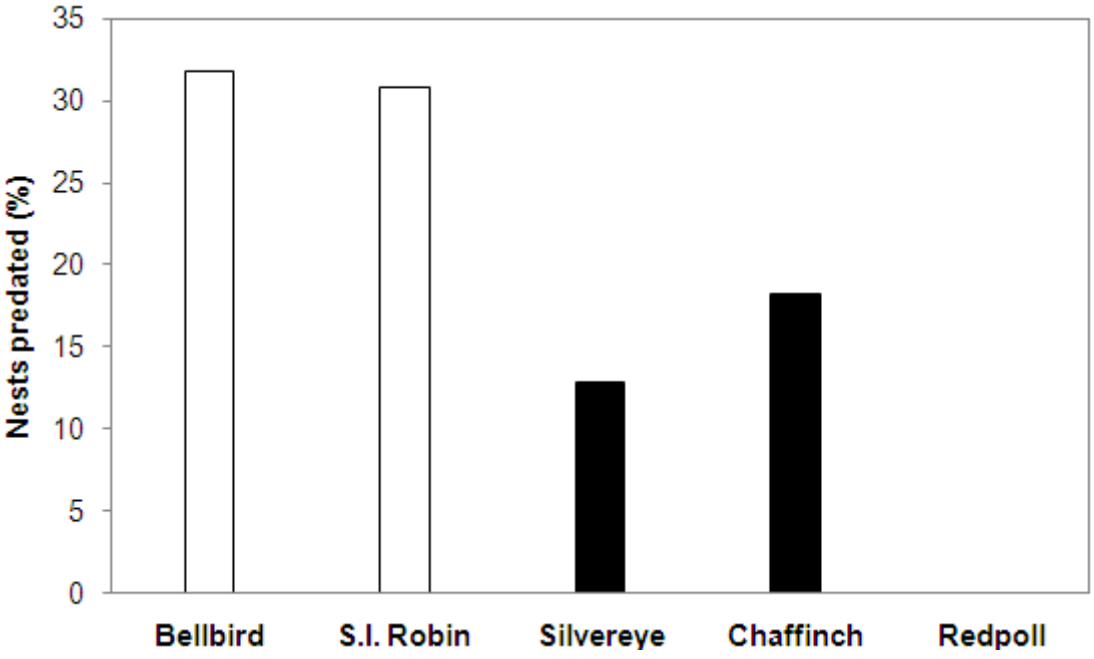

Figure 2.3. Difference in the total percentage of nests depredated for the endemic (open bars) and continental species (black bars) after six days.

Chapter 3

A comparative study of nest flushing behaviour between endemic and continental passerines in New Zealand

3.1 Abstract

Nest predation is a major cause of mortality of parental birds and their young. Birds experiencing high predation risk often have many adaptations, both direct and indirect, that reduces the probability of the parent and its offspring becoming depredated. Insular birds that evolved for a long period without predatory mammals, such as the endemic birds in New Zealand, would be expected to lack some of the anti-predatory adaptations against mammalian predators found in continental birds. I did a comparative study between endemic New Zealand birds and continental birds (which evolved with predatory mammals in their native ranges) to investigate the differences in parental behaviour after experimentally flushing birds from their nests. I simulated the threat of a potential mammalian predator to the nest by recording the response of birds to my approach while they were on the nest and incubating. Comparison of flushing responses revealed distinct behavioural differences between endemic and continental birds. Endemic birds tended to flush later or not at all, and returned to their nests much sooner after being flushed from the nest. Visitation rates to nests returned to their pre-disturbance rate in endemic birds within 30 minutes of my approach, but not in continental birds. Such differences in nesting behaviour may reflect the divergent evolutionary histories of the two different groups of birds. My study confirms a lack of anti-predator behaviour in some endemic insular birds at the nest and that this may put them at greater risk to introduced mammalian predators.

3.2 Introduction

The arrival of humans and their introduction of predatory mammals on isolated islands precipitated a wave of extinctions. Island species are vulnerable to introduced predators as isolation from continental faunas has lead to large changes in their life-history that limits their ability to cope with increased mortality rates (Clegg et al. 2002; Blackburn et al. 2004). Behavioural changes in island species can be detrimental to surviving with introduced predators, with a number of recent avian extinctions attributed to behavioural characteristics of the extinct species (Reed 1999). Species on isolated islands have long been noted as being predator-naïve, exacerbating their decline when faced with exotic predatory species. For example, a single feral dog in New Zealand was found to have killed around 500 brown kiwis (*Apteryx australis*) over a period of six weeks, highlighting this native bird's vulnerability to an exotic predator (Milberg and Tyrberg 1993). Noted behavioural changes in island birds include a reduction in flocking (Beauchamp 2004), low dispersal rates, and more frequent placement of nests on the ground (Reed 1999). These behavioural changes are likely to have played a key role in the precarious state of island faunas, not only in New Zealand, but also in avifaunas in other island archipelagos such as Hawaii, Seychelles and the Galapagos. Understanding behavioural differences between insular and continental species is thus critical for understanding the decline and extinction of insular birds.

Insular environments are isolated and generally species-depauperate environments with a low diversity of predators or even the complete absence of top predators. When isolated from predators for a long period, selection may favour the loss of costly anti-

predator behaviour in prey species (Blumstein and Daniel 2005), or a reduction in their sensitivity to predators (Lima & Dill 1990). The mechanism underlying this loss of anti-predatory behaviour possibly results from a reduction of predation risk because islands support fewer predators than adjacent continental areas (Blumstein 2002). Maintaining anti-predator behaviour in the absence of predators is assumed to be costly as many behavioural traits quickly decline following removal of predators (Blumstein 2006). A reduction in predation pressure for example, could allow individuals to increase foraging behaviour as less time needs to be allocated to anti-predatory vigilance (Hunter and Skinner 1998). In contrast, continental species that have co-evolved with a large diversity of predators should be expected to have a suite of anti-predator adaptations minimising their risk of predation. Species evolving with multiple predators may often evolve specific traits to reduce predation risk in response to each predator (Blumstein et al. 2006). As for example, Bouskila (1995) found that desert rodents that remain hidden on full moon nights to avoid owl predation may still be at risk to predation by snakes. The rodents may react to this by changing their behaviour based on the relative importance of each predator at each location. Island species that lack multiple anti-predator traits may be at risk following the introduction of additional predators to their environment.

New Zealand has been isolated from the nearest continental landmass for over 80 million years (Cooper and Millener 1993). This long period of isolation has lead to high levels of endemism in the plants and animals and shifts in life-history traits compared to their continental counterparts. Life-history changes have been evident with many species shifting niches, becoming gigantic, long-lived or reproducing slowly (Daugherty et al. 1993). For example, gigantism has evolved repeatedly among a variety of New Zealand taxa, including earthworms (*Spenceriella*), beetles (*Dorcus*, *Prionoplus*), land snails

(*Paryphanta*, *Placostylus*, *Powelliphanta*) and birds (*Dinornis*, *Strigops*, *Harpagornis;* Wallis and Trewick 2009). As with other isolated islands, New Zealand birds evolved in the absence of predatory mammals or snakes but they did not evolve in an environment completely free of predation risk. There were predators present, but these were other birds. Previous to the introduction of mammalian predators there were a variety of endemic avian predators including the laughing owl *(Sceloglaux albifacies*), New Zealand hawk *(Circus eylesi*), Haast's eagle (*Harpagornis moorei*) and the New Zealand falcon (*Falco novaeseelandiae*), of which three are now extinct. These avian predators likely exerted strong pressures on life-history traits of their prey species and probably lead to these species becoming cryptic in their colouration (Holdaway 1989). This pattern may have arisen because avian predators hunt primarily using visual cues, whereas mammalian predators rely more heavily on olfactory cues (Bittner 2003). Behavioural shifts to avoid avian predation are evident in the endemic fauna. The kakapo (*Strigops habroptilus*), for example, has become nocturnal to perhaps avoid diurnal predators and they evolved a lek breeding system which requires males to spend long periods of time on the ground. This leaves this flightless species particularly susceptible to predation from mammals and is one of the many reasons for their current critical status.

The behaviour of avoiding or fleeing from predators is one of the most important adaptations of an individual. Failure to flee from a predator can clearly result in an abrupt end to any future reproductive success, so there must be strong selective pressure on individuals to successfully avoid predators (Ydenberg and Dill 1986). For a volant bird, flight is the main means of escape but an individual must make a decision as to the appropriate time to flee. Optimal flight initiation distances are based on the economics of decisions by prey on when to flee from predators. Optimality models predict that once a

prey detects a predator, it should monitor its approach until the costs of escape and of remaining are equal, and then flee (Cooper and Frederick 2007). Flight initiation distances can thus be viewed as a cost-benefit analysis, where a trade-off is made between staying, which risks injury or death, or fleeing, which takes energy and time taken away from other important activities (Ydenberg and Dill 1986; Kramer and Bonenfant 1997). Flight decisions are context dependant and can be influenced by a range of factors including the availability of refuges, predator approach velocity (Bonenfant and Kramer 1996), starting distance (Blumstein et al. 2003), and the identity of the predatory species (Stankowich and Blumstein 2005). As optimal flight initiation distances are affected by a suite of different factors, species evolving in different predator regimes might be expected to have evolved different flight initiation distances.

Individual fleeing behaviour is not the only important factor determining avian reproductive success. In addition, behaviour of birds around the nest can affect nesting success. For example, parental activity can be costly because it can attract a predator's attention to the nest (Martin et al. 2000; Weidinger 2004). High levels of activity around a nest increase nest conspicuousness, and thereby the risk of predation (Martin et al. 2000). As a result, birds that evolved in environments with a high risk of predation tend to visit nests less frequently and have a range of behaviours that in general make it more difficult for a predator to locate the nest (Skutch 1985). These may include direct nest defence behaviours such as defensive displays (Montgomerie and Weatherhead 1988), or more indirect methods such as reduced activity around the nest during peak predation periods (Eggers et al. 2008). Broom and Ruxton (2005) suggested that nesting birds that are cryptic will have optimal flight strategies in which parents should flee immediately on seeing the predator or only to run when the predator initiates an attack. However, birds that

evolved on islands with lower predatory risk may flush late and return very quickly to the nest, thus giving their nest's location away. Island birds that lack the anti-predator behavioural defences to predators found in continental species are highly sensitive to invasive species (McLean et al. 1999). The possible lack of anti-predator defences at the nest may put endemic island birds at greater risk of predation.

The aim of this chapter is to determine if there are any behavioural differences between New Zealand's endemic birds and continental species that have been introduced to New Zealand in relation to their reaction to the approach of a potential predator. I measured differences in the flush responses and return rates (to the nest) of various endemic and continental birds. I also determined if there was a difference in parental behaviour around the nest after bird has been flushed from its nest. Given their differing evolutionary history with predators, I predicted that the endemic birds would be less prone to flush from the nest, and if they did flush, then they would return earlier with their post-flushing behaviours unlikely to change compared to birds that evolved on continental areas.

3.3 Methods

Study site and species

Parental behaviour at the nest was collected from a variety of passerine species. The study was conducted at Kowhai Bush, Kaikoura, New Zealand (173° 37'E, 42° 23'S) between the breeding seasons over two summer periods (2009-10 and 2010-11). Kowhai bush is a

240 ha low-elevation forest dominated primarily by kanuka (*Kunzea ericoides*) canopy with small pockets of native podocarp. I only used open nesting passerines to reduce the variability in flush responses due to differing types of nests (i.e., open vs. cavity nesting). The endemic species sampled were bellbird (*Anthornis melanura*), South Island robin (*Petroica a. australis*), fantail (*Rhipidura fuliginosa*) and brown creeper (*Mohoua novaeseelandiae*). The continental species sampled were chaffinch (*Fringilla coelebs*), redpoll (*Carduelis flammea*), song thrush (*Turdis philomelos*), blackbird (*T. merula*), dunnock (*Prunella modularis*), yellowhammer (*Emberiza citronella*) and silvereye (*Zosterops lateralis*). The silvereye is usually classified as a native New Zealand species, but as it evolved in continental Australia, and only colonised New Zealand during the 19th century when the rapid alteration of the landscape permitted its persistence, it is here classified as a "continental" species.

Data collection

Nests were located by following adult birds carrying nesting material or food back to the nest or by systematically searching the vegetation. Once nests were found, flagging tape along with a GPS (when possible) was used to mark the nest to facilitate later relocation. The height, position and species of tree were recorded for each nest. Long poles with mirrors attached (mirror poles) were used to view the contents of nests situated high in the canopy. Nests were only checked if either parental bird was absent from the nest. The status of each nest was recorded during each visit.

Flushing procedure

Parent birds were flushed from their nests by using my approach to the nest to mimic the approach of a potential predator. I walked in a straight line, beginning 15 m from the nest and approached until the bird flushed or I touched the nest. Walking towards the nest was done at a constant pace (0.5 m s^{-1}). The position of the bird on the nest was determined from a distance using binoculars to ensure that the bird was approached in such a way that I was visible to it as I began the procedure. In other words, I ensured that I did not approach from the rear of the bird and thus would be undetected or unseen until very close. The nests I used for approaches had a range of heights (mean = 2.61 m, SD = 1.57). For each nest approach, a mirror pole of the same height of the nest was held vertically. This simulated (for high nests particularly) that the height of the potential predator was the same as the height of the nest and thus a threat. Adjusting the pole at each nest height was necessary as nests at greater heights have a longer distance to the predator than lower nests at the same horizontal distance. Thus, parents with higher nests may perceive less threat and flush later (Cooper 2005).

The incubating bird's "visibility" from the nest was also measured. Visibility can affect flushing distance if birds with well hidden nests perceive the risk is lower, due to better camouflage, or if they do not see the approach of a predator due to the obstructions (Burhans and Thompson 2001). The level of visibility was measured by estimating the proportion of the nest that could be observed from 2 m distance at the four cardinal directions (North, East, South and West). Nest visibility was measured at eye level to the nest. This estimated the bird's field of view from the nest and not just a human's visibility of the nest. For example, the ground nests of yellowhammers nests are easily visible, even in tall grass, to humans standing >1.5 m above the nest, but to the yellowhammer,

visibility will be obscured by the tall grass. Each nest was only used once for each individual experiment and if nests of the same species were found later in the season within close proximity to a previous nest they were not used in the analysis in case this was a renest or second brood of the previous nest (most birds were not banded for individual recognition). This ensured independence of my samples and avoided pseudoreplication.

Flush distance and return rates

Flush responses and return rates involved finding active nests, flushing the attending adult(s) off the nest, and then waiting 10 minutes for them to return. All nests that were used in this experiment were at the incubation stage, and at least 2 days had passed after the last egg was laid; this ensured that normal incubation behaviour had developed. As I approached the nest and the bird flushed, the distance at which it flushed was measured. I also measured flush propensity (i.e., the likelihood of an individual to flush at an appropriate distance to avoid predation on itself or the nest) of a parent. If a bird flushed before I got within one meter from the nest it was treated as "flushed," However if a bird flushed after I got within one meter of the nest it was treated as a "close flush." The return rate was measured after retreating from the nest as far as possible (so I was still able to view the nest) and then waiting 10 minutes to see if the flushed birds returned. If incubating birds returned within 10 minutes they were treated as "returned." However, if they took longer than 10 minutes to return they were treated as "not returning."

Nest visitation and attentiveness

Behavioural changes at the nest after flushing was measured by filming nests of South Island robins and song thrushes. The nests used in this experiment were at the nestling stage, so that changes in parental time spent at the nest and feeding rate changes could be assessed. The changes in parental bird's behaviours were studied before and after the nests were flushed. Tripods for the camera were placed near the nest a day before the experiment occurred to prevent the parents being affected by presence of the camera. Cameras were set up 3 m - 15 m from the nest. They were set up as far as possible from the nest to provide a clear view of the nest. To set up the "pre" control flushing treatment, I approached the nest no closer than where the tripod was positioned. This reduced the likelihood of changing the bird's behaviour and forcing them to flush early. The camera was run for 4 hours. Two hours of filming occurring before nests were experimentally flushed (the "pre" control period) and then another 2 hours after the nest was flushed (the "post" flushing period). Flushing at the 2 hour mark followed the same protocol described above and as undertaken at the incubation stage. To control for time of day, I conducted half of my "pre" treatments in the morning and half in the afternoon after I had "post" flushed it. To avoid daily behavioural changes of individual birds (i.e. morning and evening behaviours), the camera was set up at sunrise and no more than one hour afterward.

Statistical analysis

Multifactor ANOVAs were used to compare differences in flush distance, and return rates between clutch size, nest heights, average nest visibilities, species identity, and

evolutionary origin (endemic, continental). Paired t-tests and multifactor ANOVAs were used to compare parental visitation and attentiveness differences. Logistic regressions were used to compare flush propensity and return propensity. I used a total of 109 nests for my analyses. Data on parental behavioural changes during the nestling stage were taken from 31 nests. The statistical tests were performed on the data under a critical value of $p = 0.05$. Sample sizes varied between analyses due to nest availability.

3.4 Results

Flush distance and flush propensity

A multifactor ANOVA showed that flush distances were significantly different between the endemic and continental birds (Figure 3.1; $F_{1,88} = 133.29$, $p = 0.001$) and among each species (Table 3.1; $F_{13,88} = 3.25$, $p = 0.001$). Endemic birds had smaller flush distances than continental birds. There was no significant difference in flush distances with average nest visibility ($F_{1,88} = 1.03$, $p = 0.31$), nest height ($F_{1,88} = 0.10$, $p = 0.75$) and clutch size ($F_{1,88} = 0.33$, $p = 0.80$). There was a significant interaction between origin (endemic vs. continental) and average nest visibility ($F_{1,64} = 5.22$, $p = 0.026$), and between origin and nest height ($F_{1,64} = 4.12$, $p = 0.046$). Continental birds built more cryptic nests (lower nest visibility) lower to the ground than endemic birds. However, there were no significant differences in the interaction of species and average nest visibility ($F_{9,64} = 0.48$, $p = 0.88$) or the interaction of species and nest height ($F_{8,64} = 0.76$, $p = 0.64$). The propensity to flush from the nest was significant for origin (Table 3.2: $Z = 4.63$, $p = 0.001$) and nest height ($Z = 2.12$, $p = 0.034$). Endemic birds and birds in high nesting sites “close flushed”

more often than not compared to continental birds and birds at lower nesting sites. Flush propensity was not significant for average nest visibility ($Z = 0.69$, $p = 0.49$).

Return times and return propensity

The return times of birds during the incubation stage were significantly different between the endemic and continental species (Table 3.1: $F_{1,87} = 98.74$, $p = 0.001$) and among each species ($F_{13,87} = 3.68$, $p = 0.001$). Endemic birds returned quicker to the nest after being flushed compared to continental birds. There was no significant differences in return times with nest height (Figure 3.2: $F_{1,87} = 2.41$, $p = 0.12$), or average nest visibility ($F_{1,87} = 0.38$, $p = 0.54$). Return times at the nestling stage were significantly different between the endemic and continental species ($F_{1,24} = 5.17$, $p = 0.032$), but there was no significant difference in return times with average nest visibility ($F_{1,24} = 1.25$, $p = 0.27$) or flush type (early in morning vs. 2 hours afterwards: $F_{1,24} = 2.30$, $p = 0.14$).

The propensity to return to the nest was significantly different between the two evolutionary origins (Table 3.2; $Z = 3.95$, $p = 0.001$). Endemic New Zealand birds were more likely to return to the nest within the ten minute period than the continental birds. However, return propensity was not significantly different with nest height ($Z = 1.81$, $p = 0.070$).

Nest visitation and attentiveness

The total number of visits over two hours to the nest was significantly different between the South Island robins and song thrushes ($t = 2.78$, p-value $= 0.010$). It was expected that

after being flushed from the nest, parents will reduce the rate of visitation to the nest to avoid an increased risk of predation. A multifactor ANOVA of changes in parent visitation rates after nest flushing revealed that there was no significant changes between South Island robins and song thrushes over two hours ($F_{1,16}$ = 0.18, p = 0.67) or one hour ($F_{1,27}$ =2.75, p = 0.11). There was however, significant changes in the behaviour of the birds over 30 minutes (Figure 3.3; $F_{1,25}$ = 9.60, p = 0.005). South Island robins visited the nests more often than song thrushes within 30 minutes for both the "pre" and "post" flushed experiments. Song thrushes and South Island robins differed in their visitation increase or decrease in response to being flushed. South Island robins slightly increased in their visitation rate to the nest "post"' flushing, however these results were not significant ($F_{1,25}$ = 1.51, p = 0.21). Song thrushes post flushing, reduced their visitation rates to the nest although these results were also insignificant ($F_{1,25}$ = 3.15, p = 0.09). Nest height had a significant influence on change in nest visitation rate over 30 minutes ($F_{1,25}$ = 4.68, p = 0.04) and was almost significant over one hour ($F_{1,25}$ = 3.35, p = 0.080). Flush type had a significant influence on change in nest visitation over 30 minutes ($F_{1,15}$ = 7.50, p = 0.011), and was nearly significant over one hour ($F_{1,25}$ = 3.92, p = 0.06). The total percentage time that parents spent at nests over the four hours was not significantly different between South Island robins and song thrushes (t = -0.83, p-value = 0.42). There was no significant difference between South Island robins and song thrushes in percentage attentiveness change ($F_{1,18}$ = 0.29, p = 0.59), average nest visibility ($F_{1,18}$ = 1.69 p = 0.21) or number of chicks ($F_{1,18}$ = 0.77, p = 0.39).

3.5 Discussion

I found that a variety of behavioural responses differed between my two groups of birds after flushing them from the nest. Although there were no differences in nest attentiveness before and after flushing, I did find that endemic birds that have evolved on islands responded to my flushing experiments with lower flush distances and flush propensities, quicker return rates and return propensities, more frequent nest visits and unchanged visitation rates after being flushing from the nest. These differences are interesting because the behavioural responses displayed by the endemic birds may make them more susceptible to predation. Life history theory suggests that high nest predation risk should cause changes in the behavioural responses of birds and that they should adjust their life history traits in such a way so as to reduce the likelihood of their nests becoming preyed upon by predators. Endemic birds when compared to the continental birds in this study seem to lack these anti-predatory flushing traits.

In my study, I observed that the distance at which a bird flushed from its nest depended on its evolutionary origin, that is, whether the bird had evolved in New Zealand or on a continental. Blumstein and Daniel (2005) reported contrasting results with their study of island marsupials. They found that the flight initiation distances of Macropodinae species (kangaroos, wallabies, pademelons, etc.) on islands was not consistently different to that of the mainland species, with the "flightiness" of the individual often experience-dependant, and insensitive to both the effects of island isolation and predator regimes. It is not clear why this result is different from what I observed, although in most cases, the marsupial species studied by Blumstein and Daniel (2005) were conspecific with those on the mainland, while in my study, I used insular species that were endemic at the specific

level or higher, and thus likely to have evolved for a longer period in the absence of mammalian predators**.** Experience-dependent behaviours may change rapidly following the introduction of predators, whereas more hard-wired behaviours may persist for many generations. Behaviours such as flight initiation distance can be very flexible as found in the insular Macropodinae animals but may also be more hard-wired as found here in endemic New Zealand birds. This suggests flight initiation distance is modified both by experience with predators and genetic hard-wired behaviours.

There were clear differences in the flush distances between the two groups and between birds in my study. This is expected, given that different birds are likely to differ in their life history strategies, even within each of the two groups. The two ground nesting species I sampled (yellowhammer and dunnock) for example, were expected to flush as soon as they see/saw a potential predator compared to tree nesting species due to the higher risk from approaching mammalian predators (Rodgers and Smith 1995). The interactions I found between evolutionary origins with average nest visibility and nest height indicate that continental birds may assess their surroundings when deciding to flee from predators. This is similar to previous studies that show birds use the degree of nest concealment in their escape decisions when potential predators approach (Burhans and Thompson 2001; Albrecht and Klvaňa 2004). Contrary to parental investment theory, clutch size did not affect flushing distance. It is likely that a distinction between broods or mean egg volume was needed to fully capture the measures of reproductive values of each clutch.

A recent study by Berger et al. (2007) found that insular animals can develop adaptations to novel predators. Endemic marine iguanas that had been isolated from predators for millions of years were found to have developed anti-predator behaviour after

several decades with introduced predators through increased flight initiation distances and changes in escape responses. This suggests that flight behaviours are experience dependant and endemic species have modified their behaviour to novel predation threats. However, even though the reaction was present the strength of the flight responses was very low. Thus although the iguanas adjusted their anti-predator behaviour, the low behavioural plasticity of the species suggests that the behavioural adjustments are unlikely to sufficiently lower the risk of predation. Some insular endemic birds also show phenotypic plasticity with novel predation risks (Massaro et al. 2008; Peluc et al. 2008). Behavioural plasticity is a major determinant of the invasion success in birds adapting to novel situations very quickly (Sol et al. 2002). Although some New Zealand birds may be able to adapt to novel predator threats, the lack of plasticity in their anti-predator flushing behaviours compared to the flexible behaviours of introduced species may limit the strength of nest flushing distances leaving endemic birds more susceptible to mammalian predators.

Future studies of endemic and continental birds in New Zealand could include more realistic nest flushing scenarios such as leading dogs to nests to see if there are any changes in the relative strength of nest flushing distances in endemic compared to continental birds. A study by Lord et al. (2001) on New Zealand dotterels found that shorebirds can become habituated to humans but perceive dogs as posing more of a threat than humans on foot with their avoidance response much greater. A comparison with live predators would be useful to determine if endemic birds elicited such weak responses to my flushing experiments because the study site has been used for research in the past and my sample of birds may have included individuals already habituated to humans. The use

of alternative predators could more accurately measure nest flushing differences between endemic and continental birds.

The propensity to flush from nests significantly varied with the evolutionary origin of the species. Endemic insular birds often did not flush at all from the nest even when the nest was touched. Birds also flushed less often with higher nest heights which may relate to the nest concealment and escape decisions as discussed above. Broom and Ruxton (2005) reported two optimal strategies for prey individuals: either to run as soon as they detect a predator approaching or to only flee in response to having been detected by the predator. Both are costly strategies, with fleeing in most cases alerting the predator to the presence of the prey individual, and increasing the risk that the predator may attack. The countervailing strategy for the prey to sit tight relies on its crypsis, with the bird only fleeing if it perceives that the predator has detected it and is about to attack. For nesting birds, this strategy may be very costly as, if identified by the predator, both the parent and its offspring will be vulnerable to becoming depredated. It also may allow the prey to survive simply because the predator passes by without detecting the prey's presence. New Zealand's avian predators such as the New Zealand hawk and the New Zealand falcon primarily hunt (or hunted) by chasing birds in flight, probably swooping from high branches and flying through the forest in pursuit of their prey (Diamond and Bond 1999). Flushing from nests with these predators instead of remaining cryptic on the nest would likely reduce the chances of survival. It is possible that small endemic passerines co-evolving with avian predators have evolved 'non-flushing' tendencies to avoid predation from aerial avian predators. It would be interesting to investigate differences in flush propensities of insular and continental birds when coupled with multiple predator species (i.e., avian, mammalian, reptilian).

In this study, the time at which the bird returned to the nest after it had been flushed depended on the evolutionary origin of the species, with endemic birds returning to the nest much quicker than continental birds. This was found at both the incubation and nestling development stages. There was also a tendency for continental birds not to return after 10 minutes. Parental visits to the nest can increase the risk of predation to both parents and eggs or young by attracting the attention of predators (Ghalambor and Martin 2001). Skutch (1949) hypothesised that high nest predation may favour less frequent parental visitation to nests because it may lower the probability of discovery of nests by predators. However, at the incubation stage, birds may be limited in their time spent off the nest, with their return times needing to remain above the presumed threshold (25°C to 27°C) for embryonic development (Weathers 1989). Once birds have been flushed off a nest they may try to maximise reproduction potential by using a trade-off where they stay off the nest long enough to allow a potential predator to leave the surrounding area but not long enough to lower egg temperature below the embryonic threshold. The quick return times of endemic species would suggest that insular birds seem to lack this trade-off behaviour. Mammals now present on New Zealand may exploit this behaviour and both parents and offspring would be in potential danger. As many introduced birds did not return after 10 minutes in the incubation experiment it would be worth continuing this aspect of the study to determine whether the continental birds use a trade-off in deciding when to return to the nest after being flushed.

There was a significant difference between the total numbers of visits to the nest over two hours with endemic birds visiting the nest more often than continental birds. Previous studies have shown support for the parental visitation hypothesis, that parents experiencing high predation risk decrease rates of nest visitation (Eggers et al. 2005;

Eggers et al. 2008) and increase their nest attentiveness (Fontaine and Martin 2006). Endemic birds visited their nests frequently (once every four minutes) to provide for their nestlings. Compared to the endemic species, continental birds had lower visitation rates (once every 7 minutes) to their nests. These differences may reflect the different environments in which the two groups of species evolved. Eggers et al. (2005) reported that Siberian jays (*Perisoreus infaustus*) can assess and change their number of visits based on predation risks by increasing food load sizes and lowering visits during predation prone periods. Isolated island species that have lower predation intensities may lack the selective pressures that allow them to assess risks and respond accordingly. It would be interesting to investigate the food loading differences in insular and continental birds in different predation intensities.

My results have shown continental birds reacted to the flushing experiment with nestling visitation lower after exposure to the flushing experiment, whereas endemic birds did not seem to respond and their visitation rates remained unchanged. This supports Eggers et al. (2008) who found that model presentations of a predatory bird may temporarily terminate parental visits the nest. My nest flushing disturbance changed the behaviour of the introduced birds for only a short period of time with there being no significance after one hour of observation. It is likely that the continental birds returned to 'normal' behaviour quickly due to the large amount of investment in the nestlings. Flush type (early in morning vs. 2 hours afterwards) was also a significant factor in the parental visitation rates. Knapton (1984) reported that parents feed nestlings more frequently in the morning and evening than during the rest of the day. Flushing half of my samples at sunrise may have more effect on the birds' behaviour than later in the day but as both endemic and continental birds were both flushed similarly the differences should be

attributed to the differences in the behaviour of two groups of birds. Nest attentiveness was unchanged between the endemic and continental birds. Nest attentiveness is thought to influence nest predation by hiding eggs or nestlings but is highly dependable on nestling stage (Schaefer et al. 2005). It may be probable that the differences in nestling stages of my samples obscured the effect of continental behavioural changes after flushing.

The behaviour of insular and continental birds around the nest are likely to have been under different selective pressures in their evolutionary past given the differences in the two environments. The result is changes in many behavioural traits, which function in increasing the survival of their offspring and lowering their risk of predation. This study has shown that there are behavioural differences between endemic and continental birds around the nest. The underlying differences seem to reflect the different predator regimes in which the two bird groups evolved. The lack of changes in anti-predatory behaviours around the nest are surprising considering that the birds of New Zealand have been exposed to mammalian selective pressures since the introduction of kiore (*Rattus exulans*) around 1000 years ago (Holdaway 1989) and even more so since the introduction of mustelids (M*ustela* spp.) and possums (*Trichosurus vulpecula)* around 140 years ago (Holdaway 1999). However, it is possible that some changes may have occurred in this time period but studies of populations that have never been exposed to introduced mammals (such as on some offshore islands) are needed to confirm this.

Future studies could investigate the differences in nesting behaviours of island birds evolving in a wide array of different predatory regimes. Stankowich and Blumstein (2005) found that flight behaviours often depended on the predatory species involved. Birds on islands may evolve different behaviours when co-evolving with avian predators compared to mammalian predators or reptilian predators. Co-evolving with one group of

predators may make an island species even more susceptible to another group of predators (if they establish on the island). It would also be beneficial to examine if there are any nesting differences between endemic birds that have survived on the mainland and endemic birds that only persist on offshore islands. There may be differences in the behavioural flexibility of some endemic birds that allow some to persist while others become extinct without management from conservationists. Furthermore, studies on nest flushing behaviours need to control for the differences in phylogeny that has constrained my analysis. As my sample species were from largely different taxonomic groups with all of the continental species sharing a more recent ancestor than they do with any of the island species, testing more closely related island and continental species would reduce the errors that result from using species from distantly related phylogenies. The results of this study have shown that the anti-predatory behaviours of endemic birds are often lacking possibly due a long evolutionary history without mammals. This reiterates that protection for endemic birds at the nest is crucial for the long-term survival of many species.

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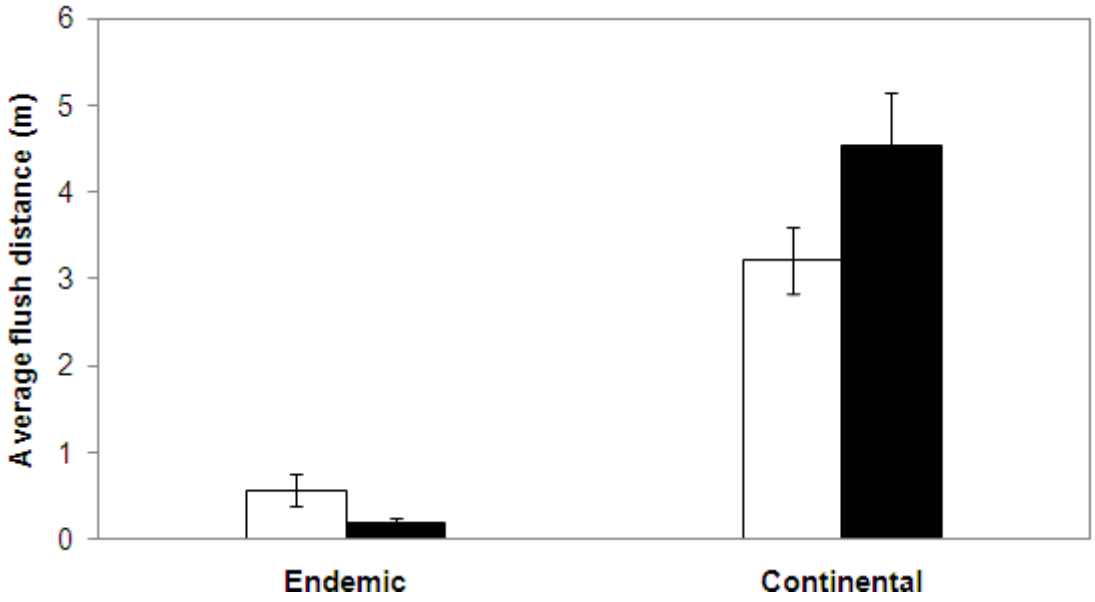

Figure 3.1. Differences in average flush distances of endemic and continental birds with average nest heights under 50% nest visibility (open bars) and over 50% nest visibility (black bars). There was a significant difference between the flush distances between the two groups. Standard errors are shown.

Table 3.1. Average flush distances and return times of the endemic and continental species sampled with standard errors. Sample sizes are given in parentheses.

Species	**Flush distance (m)**	**Return times (mins)**
Endemic species		
South Island robin (10)	0.30 ± 0.02	4.21 ± 0.34
Fantail (19)	0.18 ± 0.01	1.63 ± 0.13
Bellbird (7)	0.90 ± 0.17	6.23 ± 0.44
Brown creeper (3)	0.44 ± 0.03	5.99 ± 0.17
Continental species		
Silvereye (9)	2.09 ± 0.20	6.81 ± 0.39
Song thrush (21)	5.07 ± 0.11	9.40 ± 0.06
Dunnock (7)	3.01 ± 0.29	8.30 ± 0.35
Redpoll (12)	2.35 ± 0.21	6.30 ± 0.31
Blackbird (9)	5.06 ± 0.33	9.80 ± 0.07
Chaffinch (9)	1.96 ± 0.21	8.10 ± 0.35
Yellowhammer (3)	9.13 ± 1.90	10.00 ± 0.01

Table 3.2. Percentage of "close flushes" (propensity to flush from the nest) and "returning" (propensity to return to the nest) birds to the nest of the endemic and continental species sampled. Sample sizes are given in parentheses.

Species	**Close flush (%)**	**Returned to nest (%)**
Endemic species		
South Island robin (10)	100	90
Fantail (19)	100	100
Bellbird (7)	86	86
Brown creeper (3)	100	100
Continental species		
Silvereye (9)	33	55
Song thrush (21)	0	24
Dunnock (7)	0	57
Redpoll (12)	50	58
Blackbird (9)	11	11
Chaffinch (9)	33	33
Yellowhammer (3)	0	0

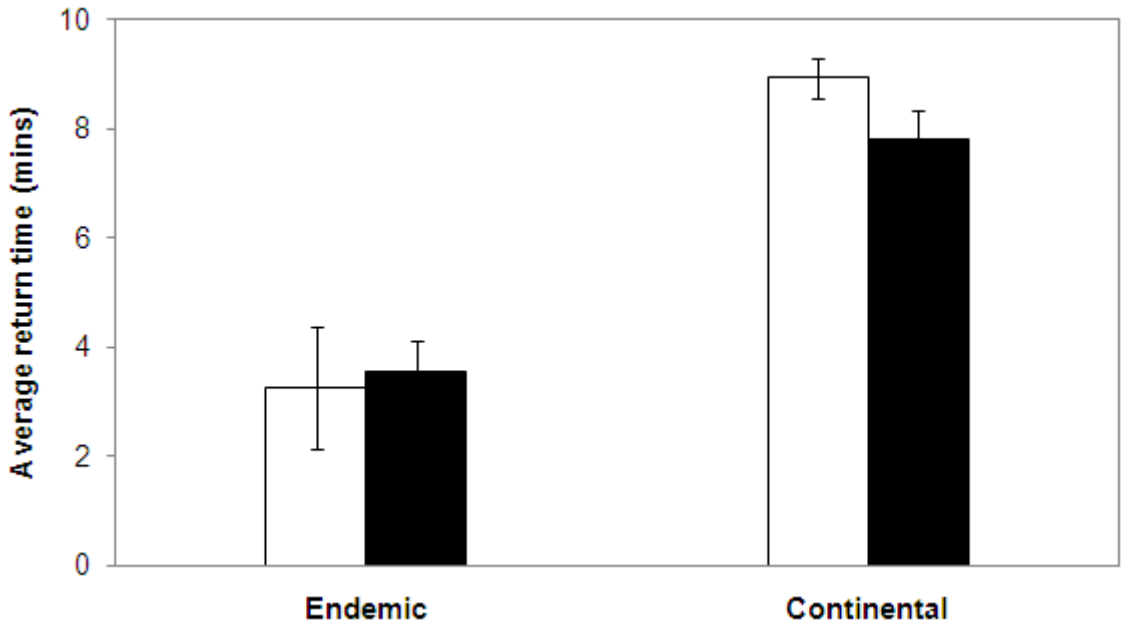

Figure 3.2. Differences in average nest return times after being flushed (with eggs) for the endemic and continental birds with nest heights less than two metres (open bars) and more than two metres (black bars). There was a significant difference between the return times between the two groups. Standard errors are shown.

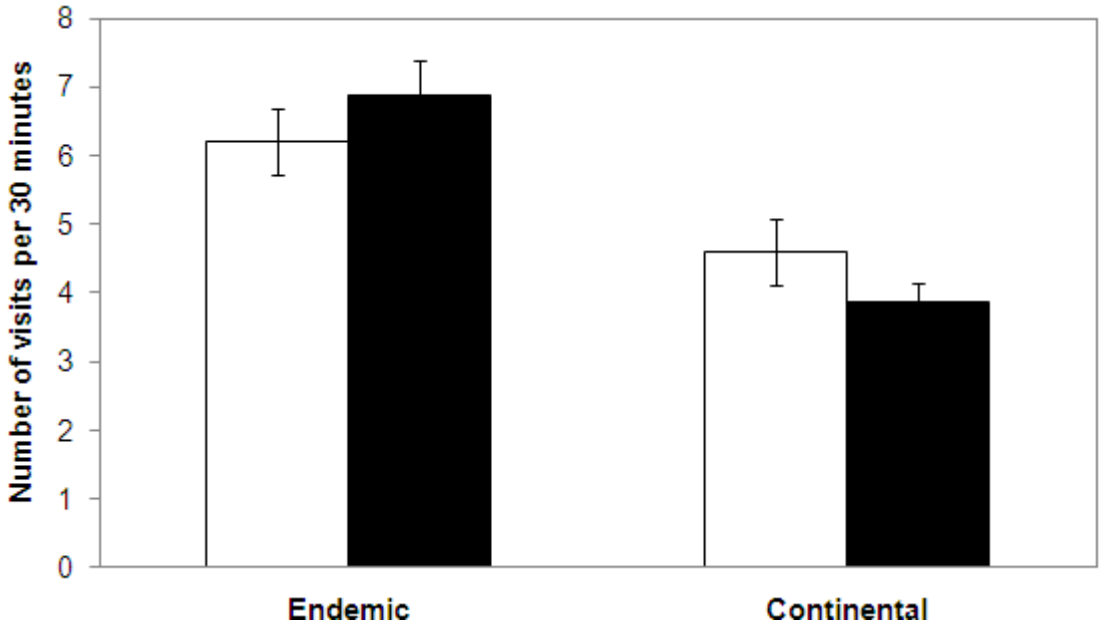

Figure 3.3. Changes in the endemic and continental bird's parental visitation rates to the nest (per 30 minutes) before flushing ("pre" flushing; open bars) and after flushing ("post" flushing; black bars). There was a significant change in the visits between endemic and continental birds. Standard errors are shown.

Chapter 4

Nest sizes changes in insular passerine birds

4.1 Abstract

Species on isolated islands often show remarkable life-history differences compared to phylogenetically-related continental species, with changes in their behaviour, morphology and reproduction. My study investigated whether island species of birds build different-sized nests compared to continental species. Nest size data was collected from island birds all over the world and compared against continental species using robust phylogenetic methods. Using a paired analysis, I found that species with cup-nests on islands built nests with significantly larger internal diameters and overall nest 'sizes' than their continental relatives. Furthermore, this pattern held when I considered only island birds of continental origin (continental 'islands' such as New Zealand and New Caledonia), which built wider nests, both internal and external diameters and larger overall nest sizes than continental Australian species. These results confirm that island environments can affect the evolution of nest architecture as well as other life history traits associated with reproduction. Insular birds, without the constraints faced by continental species may build larger nests to increase the hatching and fledging success of their young through increased insulation and increased nest stability and endurance. However, with the large number of predatory species now introduced on islands, large nests may now make island birds more vulnerable.

4.2 Introduction

Island ecosystems and their constituent species have many unique features that distinguish them from their counterparts on continental landmasses. Apart from smaller and simpler ecosystems on islands, insular species often differ in their life-histories with different body sizes and different behaviours compared to corresponding species in continental areas (Daugherty et al. 1993). These differences have been proposed to have played a key role in the rapid decline of biodiversity on islands over the last few centuries and the rapid increase in the current number of extinct and threatened species on islands around the world (Steadman, 1995; Simberloff 2000). However, understanding the differences between insular and continental species, and if these differences have played a role in the decline of biodiversity on islands, requires detailed knowledge of the life-histories of island species.

In response to the unique selective pressures of the insular environment, many animal and plant species appear to have undergone a variety of evolutionary changes on islands that set them apart from their continental relatives. These selective pressures can result in a cascade of changes in life-history traits called the insular syndrome (Thiollay 1993; Alder and Levins 1994). Insular species often show repeated patterns of change, such as small herbaceous plants becoming tree-like, birds and insects becoming flightless, animals becoming more sedentary, and behavioural shifts in some animals including tameness and lowered aggression (Blondel 2000). Many insular mammals also show a morphological pattern of becoming either dwarves or giants in comparison to their continental relatives (Lomolino 2006). This pattern was first described by Foster (1964) and labelled as the ‘island rule’ by Van Valen (1973).

The generality of the island rule has been a contentious issue, with some researchers finding exceptions to the rule (e.g., carnivores: Meiri et al. 2004; Meiri et al. 2006; Raia et al. 2006; Meiri et al. 2008) while others have confirmed it for a diversity of taxa (Lomolino 1985; Clegg and Owen 2002; Boback and Guyer 2003; Lomolino 2005). These insular patterns are often assumed to reflect the influence of island isolation and area on the strength of selective pressures such as a reduced number of inter-species interactions and increased resource limitation. Lomolino (2005) attributed the island rule to the selective forces switching from those closely associated with interspecific pressures on continents (i.e., higher levels of parasitism, predation and interspecific competition) to those related with increased intraspecific competition on islands for limited resources and ecological release (i.e., from parasitism, predation and interspecific competition). These selective pressures may explain why small mammals on islands often grow larger to utilise a broader niche range (advantageous in resource-limited islands) and enhance metabolic efficiency, while large mammals grow smaller to reduce resource requirements, increase reproductive output (Meiri et al. 2008) and increase thermal efficiency (Clegg and Owens 2002). This ultimately may result in insular species converging on an 'optimal' medium-sized body as an adaptation to low predation and high intraspecific competition for resources.

Studies of insular birds have often concluded that they respond differently to mammals with regards to the island rule. For example, some studies have found a general pattern of increased bill size in island birds (Grant 1965; Grant 1968). In contrast, Clegg and Owen (2002) found no evidence for increased bill size but showed that both bill and body size in birds follow the island rule. They suggested that shifts in bill size were associated with feeding ecology while body size changes related to intraspecific

competition and thermal ecology. The differences between studies may arise because of the disproportionate number of small passerines used in earlier analyses. Nevertheless, morphological changes in insular species have been found to occur within relatively short temporal scales, with recently colonised island populations of the silvereye (*Zosterops* spp.*)* exhibiting larger body sizes than on the Australian mainland (Clegg et al. 2002).

In addition to morphological changes, breeding ecology can also differ between insular species and their continental counterparts. Blondel (2000) reviewed studies on insular and mainland blue tit (*Parus caeruleus*) populations and found that individuals in insular populations laid their eggs later, had a lower clutch size, a higher number of fledglings per pair, a higher mass per fledgling, a longer nestling period, and a higher yearling survival rate. An extreme case of reproductive differences between insular and continental species is illustrated by comparing the Seychelles warbler (*Acrocephalus sechellensis*) with the continental great reed warbler (*A. arundinaceus*). The insular Seychelles warbler lays a clutch size of one, has an annual adult survival of 81% (Komdeur 2003), fledges an average of 0.32 young per pair, and has a mean life expectancy of 3.9 years (Komdeur 1994). This contrasts with the great reed warbler whose clutch size is 5.38, with a fledging success of 89% (Bensch 1996). These differences in fitness-related traits have often been interpreted as trade-offs among life history traits (Cody 1966). High intraspecific competition and a lack of predation on islands may be expected to lead to trade-offs in the reproductive strategy of insular birds that could favour reduced investment per breeding attempt in order to increase competitive ability and adult survival.

Although a number of studies have examined the morphology and breeding ecology of insular birds, there have been no attempts to determine how the island

environment has influenced the evolution of nests. Avian nests are reproductive constructions that function to provide protection to developing eggs and young (Palomino et al. 1998). For most species, the nest is the focal site for reproduction and its characteristics (e.g., size, composition, architecture) are key to successful breeding. Nest building behaviour and construction are largely genetically determined with many factors influencing the overall nest structure (Møller 1989). The evolution of nest structure may involve trade-offs between the benefits and costs of building a nest including nest sizes and their conspicuousness to predators (Møller 1990), and between energy expenditure and predation risk during nest building (Soler et al. 1998). For example, selection for smaller nests may be limited by the benefits that occur with a big nest: less crowding and reduced intrabrood competition (Slagsvold 1982*a*), and higher stability of eggs and nestlings (Slagsvold 1989*a*). On the other hand, large nests may be more conspicuous and in regions with a high predation risk, smaller nests may be advantageous despite increased crowding and risk of falls.

Compared to continental landmasses, most small oceanic islands possess an impoverished predator fauna, and thus most insular birds evolved with a low diversity of predators on both adult birds and their nests (Blackburn et al. 2005). Snakes and mammals, often the top nest predators on continents, tend to colonise islands poorly and were historically absent from most isolated islands (Cody 1966). This suggests that selection for reduced nest size to minimise predation risk may have been relaxed in island environments, and may have instead favoured an increase in the size of the nest to increase nestling survival and reduce energy expenditure in maintaining nest temperature. Insular populations often show a shift towards a more K-selected life-history (Adler and Levins 1994), and increasing the size of the nest to increase egg and nestling survival may be

another example of this pattern. On the other hand, larger nests may absorb more moisture, and are more exposed during periods of adverse environmental conditions (Slagsvold 1989*a*; Slagsvold 1989*b*), which may be more frequent on small islands. Thus differences in predation pressure and environmental conditions between islands and continents could lead to changes in the nest size of insular birds.

Although there has been much interest in the evolution of nest size, there has not been any systematic broad-scale investigation on differences between the nests of mainland and island birds. In this chapter, I survey the nest size of a wide variety of island and continental bird species. I use a pair-wise comparative study to assess changes in nest size while controlling for potentially confounding effects of phylogeny, body size, clutch size and latitude. My objective is to determine if there is any change in nest sizes in island birds when compared to their closest phylogenetic relatives on continental landmasses. My study primarily seeks to investigate the ways that the nests of insular passerines have changed, but I also search for the underlying causes of these changes.

Methods 4.3.

Comparative methods

A pairwise comparative method was used similar to that described by Møller and Birkhead (1992) and Fluen (2008). Species pairs were selected where one member of the pair was from the 'continent' (landmasses the size of Australia or larger) and the other pair member was from the closest 'island.' Species were phylogenetically paired with only close

relatives selected for comparison (see below). Each species pair was assumed to be a single and evolutionary independent unit (i.e., changes in the breeding ecology of one species pair was independent of any other species pair). This limited the use of insular birds where extensive adaptive radiation has occurred to just one species pair per clade and to ignore other species in the clade (e.g., *Acrocephalus* spp.), but this was done to avoid pseudo-replication and was considered a conservative approach to avoid any artefacts due to phylogeny. Any difference in the nest size between the two species of a pair was then assumed to have evolved after the species shared a common ancestor.

My first assessment examined the changes in the nest size of species on small, mostly volcanic islands. Using data from the literature, I compiled data on nest size for birds on the following islands: Canary, Cape Verde, Christmas, Cocos, Comoros, Cook, Fernando de Noronha, Fiji, Galapagos, Guam, Hawaii, Henderson, Lord Howe, Príncipe, São Tomé, San Andrés, San Clemente, Santa Cruz, San Miguel, Seychelles, Soccorro, Socotra and St. Lucia. I limited this analysis to small islands as large islands can often be 'mainland like' in terms of predator numbers and competitor species, with species on islands larger than 50,000 km^2 usually evolving similar body size as mainland species (Meiri et al. 2008). The largest island in my study was Viti Levu (Fiji) which is 10,531 km^2. My assumption was that any differences in the nest size between birds on these islands and their closest phylogenetic relatives on the continents can be assumed to have evolved after the ancestors of the pair colonised the island. Many small Caribbean and Indonesian islands, as well as large islands (e.g., New Guinea, New Zealand), were not used in this first analysis as they are of continental origin and thus the breeding ecology of birds in these areas may have already been divergent before the two landmasses split. Some 'continental' islands (e.g., New Guinea, Madagascar) also usually retain vestiges of

a mammalian and reptilian fauna that would create selective pressures from predation similar to that experienced by their counterparts on continental areas.

My second assessment examined the changes in the nest size resulting from different predator regimes on areas of continental origin. In this part of the study, I compared the nest sizes of birds from two 'continental' islands which are islands that were once connected to continental landmasses but are now isolated. The islands of New Zealand and New Caledonia were once part of the Zealandia landmass, which rapidly drifted away from the Australia-Antarctic region of Gondwana beginning 82 million years ago (Cooper and Millener, 1993). The avifaunas of these two islands evolved in isolation for millions of years with the Tasman Sea (New Zealand) and South Pacific Ocean (New Caledonia) preventing a number of species from reaching the islands. Despite their continental origin, the predation regimes in these islands were very different from the Australian continent in that there were no native mammalian predators, and only a limited number of potential reptilian predators. This contrasts to continental Australia which has a high diversity of avian (e.g., raptors, owls), mammalian (e.g., quolls, native rodents) and reptilian (e.g., snakes, lizards) predators that are an important source of mortality on both adults birds and their nests. Thus the apparent differences in nest size between the Australian and continental island species pairs may reflect the differences in predator regimes during their evolutionary history.

Species pairs were selected according to specific criteria. The species used in this analysis were restricted to open-nesting (nest cups) or domed-nesting passerine birds. Cavity-nesting species were not included because cavity nests will be ultimately limited by the tree cavity size and it is unclear whether the size of potential cavity nest sites differs systematically between island and continental environments. I also limited my sample to

passerine birds as they have undergone a high degree of adaptive radiation (Collias 1997) and most build highly elaborate nest structures compared to many non-passerines. For each island species, I paired it with its closest phylogenetic relative on the nearest continental area. For example, birds in São Tomé were paired up with their closest phylogenetic relatives in continental Africa. Species pairs included species that were conspecific (same species but different subspecies), congeners (same genus), or within the same subfamily. I did not use species that were the same subspecies as they are likely the result of very recent colonisations. Adaptive radiation in some bird groups is notable in many islands (e.g., Hawaiian honeycreepers, Galapagos finches). This creates a problem in selecting an appropriate species with which to compare to the closest continental relative. I took the conservative approach, and limited my analysis to selecting only one species from clades that underwent an extensive adaptive radiation. The species I selected to pair in these situations were the ones that had the most data available for the parameters being compared. Information on the taxonomy of island birds and their closest continental relatives was obtained from Dickinson (2003). In some situations, the closest relative was not available due to insufficient data so I used the closest available phylogenetic relative that was possible. These rules for selecting species for my analyses means that any observed changes in nest size are likely to correspond to the formation of new subspecies, species and endemic genera on islands, and thus one might expect nest size to also reflect any adaptations for island conditions.

I relied on published literature for my estimates of nest dimensions (Cramp and Brooks 1988; Cramp et al. 1994; Fry et al. 2000; Higgins et al. 2001; Higgins et al. 2002; Higgins et al. 2006). Other data that I used in my analyses included body size, clutch size and latitude. Body size for most species was ascertained using the latest edition of the

CRC handbook (Dunning 2008). Latitude and clutch size was found in the published literature where available. I calculated the latitude of species by averaging the upper and lower latitudes of the breeding ranges of each species. Overall, I used a total of 41 species pairs in my paired analyses (appendix 1).

Nest size

Nest sizes were described by four linear measures of nest dimensions (inner diameter, outer diameter, inner depth and outer depth). Nest mass can also be used as an index of nest size, but there was not enough data in the literature available to include this variable in my analysis. I analysed each nest dimension separately, and then calculated a general 'nest size' estimate. The nest size estimate was calculated by squaring all dimensions then subtracting the inner cup (inner diameter * inner depth) from the outer cup (outer diameter * outer depth). Due to lack of internal dimensions data for domed-nesting birds, the area estimates were based solely on the outer domed dimensions.

Statistical analysis

Sign tests were performed to compare the numbers of species pairs that changed in nest dimensions between island and continental areas. Paired sample t-tests were also performed when the data was normally distributed. All data (excluding latitude) was log transformed to normalise the data. The critical value was set at $p = 0.05$. Information on each variable was unavailable for some species in a pair so my sample size differed from one analysis to the next.

4.4 Results

Island and continental cup-nesting species

Cup nest size, an inclusive measure including the four different nest size dimensions, was significantly different between island and continental birds (Figure 4.1; Sign test: $p = 0.004$, $n = 16$). Of the 16 species pairs with information on nest size, 14 showed an increase on islands while 2 showed a decrease. Internal diameter was also significantly larger on islands (Sign test: $p = 0.019$, $n = 19$). Island birds built wider internal nest cups with 15 of the 19 species pairs larger than their continental species pair. However, both outer nest diameter (Sign test: $p = 0.11$, $n = 25$) and outer nest depth (Sign test: $p = 0.13$, $n = 22$) did not differ significantly between island and continental species. Interestingly, internal nest depth showed the opposite trend to other nest dimensions in being deeper in continental species, with only 6 island species increasing on islands and 16 decreasing in size. However, this was not quite significant (Sign test: $p = 0.052$, $n = 22$).

Island and continental domed-nesting species

Species building domed nests showed no significant differences in nests sizes between the island and continental species. The external diameter (Sign test: $p = 0.125$, $n = 7$) external depth (Sign test: $p = 0.99$, $n = 7$) and nest size (Sign test: $p = 0.69$, $n = 7$) were not significantly different between island and continental species. Island species generally built smaller domed nests than continental species pairs with only 2 out of seven island species building larger domes (figure 4.2). However, the small number of domed species

in my sample means that I would be unable to detect any changes unless all by one pair showed the same pattern.

Island and continental life-history traits

Island and continental species in my study differed in a number of life-history traits (table 4.1) and these could potentially confound the analyses of nest size above. A regression of clutch size with nest size showed that clutch size was significantly and positively correlated with nest size for both cup ($t = 2.46$, $df = 1, 38$, $p = 0.018$) and domed nest sizes ($t = 3.69$, $df = 1, 11$, $p = 0.004$). However, clutch sizes of island species were significantly smaller than their continental relatives (Sign test: $p = < 0.001$, $n = 32$), with island species laying clutches ~0.76 eggs less on average than continental species (table 4.1). Thus, the larger nests of island species were not due to large clutches on islands and in fact the reverse was true: island birds built larger nests despite laying smaller clutches than continental species.

A regression of body size and nest size also revealed that body size was significantly and positively correlated with nest size for cup nests ($t = 13.36$, $df = 1, 38$, $p = < 0.001$). Domed-nesting species showed a similar trend but this was not significant ($t = 2.01$, $df = 1, 12$, $p = 0.067$). However, there was no significant difference between the body sizes of island and continental species in my sample (Sign test: $p = 0.99$, $n = 34$). Thus, although nest size is related allometrically to body size (i.e., bigger species build bigger nests), the larger nests of island species is not due to island birds having a larger body size.

There was a significant difference between the mean latitudinal range of the two groups of paired species (Sign test: p = < 0.001, n = 27). Island birds in my sample were frequently more equatorial (i.e., closer to the equator) than their continental relatives with only 6 of 34 species pairs in which the island species was more temperate. However, regressions of latitude and nest size showed no significant relationship for either cup (t = 1.74, df = 1, 38, p = 0.089) or domed-nesting species (t = -1.62, df = 1, 12, p = 0.13). Thus, the larger nests of insular species do not appear to be the result of differences in latitude from their continental counterparts.

'Continental' island and Australian cup-nesting species

Analyses of my continental island and Australian species pairs confirmed the pattern in nest size I found above with my analysis of oceanic islands. The external diameters of the continental island species nests were significantly larger than their Australian relatives (Figure. 4.3; Sign test: p = 0.02, n = 7). Of the 7 species pairs, all 7 island species built wider external nest cups. Both the internal diameters and overall nest sizes of the island species showed a similar trend, with 5 of the 6 species pairs building larger nests on islands, however these were not significant (Sign test: p = 0.22, n = 7), probably due to the small sample size. The external (Sign test: p = 0.99, n = 7) and internal (Sign test: p = 0.69, n = 7) nest depths were not significantly different between the two treatments of species pairs. I performed paired t-tests to assess the magnitude of differences between continental island and Australian species and found that island species pairs built larger nests for the external diameter (t = -6.20, df = 5, p = < 0.001) and overall nest size (t = -2.57, df = 5, p = 0.050).

'Continental' island and Australian life-history traits

The continental island and Australian species pairs in my study showed similarities in life-history traits (table 4.2). Body size (Sign test: p = 0.99, n = 7), clutch size (Sign test: p = 0.45, n = 7) and latitude (Sign test: p = 0.45, n = 7) were not significantly different between the continental island and Australian species. Regressions analysis showed that body size was correlated with nest size (t = 4.52, df = 1, 11, p = < 0.001), but neither latitude (t = 2.01, df = 1, 11, p = 0.07), nor clutch size was correlated with nest size (t = 1.23, df = 1, 11, p = 0. 24). Thus, the larger nests of birds on continental islands does not appear to be the result of differences in clutch size, body size or latitude between the two groups of species.

4.5 Discussion

I found that nest size was significantly different between island and continental cup-nesting birds. Island birds built nests that were both larger in individual nest dimensions and larger in overall nest size. Island domed-nesting birds however, showed no such nest size increases. The comparisons of continental island and Australian species yielded similar results with island birds building wider nest cups (both external and internal diameters) and overall larger nest sizes. My comparative survey confirms that insular birds built nests that differ from that of their continental counterparts. It seems likely that these

differences are the result of the different selective pressures found in insular environments which favour changes in nest structure.

Islands environments can be quite different from that on continents, and are especially depauperate in terms of the number of predatory species which can increase population densities of prey (Cody 1966). The life-histories of insular species may thus be highly affected by intraspecific competition, favouring a reduction in clutch size and increased investment into building larger, thicker nests that provide more insulation and increase reproductive success. The architecture of the nest has been suggested to alter incubation potential (Collias 1986) with both nest depth and floor thickness known to play a role in increasing nest incubation efficiency (Skowron and Kern 1980). Reid et al. (2000) manipulated the thermal properties of starling (*Sturnus vulgaris*) nests and found that increased insulation saved parental resources (e.g., less time incubating) which was reallocated to later stages of the same or future reproductive attempts. The larger nests of island birds that I found in my study may thus be a consequence of investing more in nest construction to reduce the energetic costs of incubation. A comparison of the thermal properties of nests of island and continental birds would be worthwhile to test this hypothesis.

If nest construction influences a nest's thermoregulation qualities it is unclear as to why island birds built wider internal cups. Slagsvold (1982*b*) found that parents that build large nests can rear a greater number of young (due to less crowding and competition in the nest) compared to parents that build smaller nests but also that wider nests had lower hatching success. This is attributed to wider nests having a larger surface area and being more exposed to the weather during incubation. Insular environments are known to be relatively stable with infrequent extreme climatic events, allowing populations to persist

for millions of years (Cronk 1997). The relative climatic stability may allow island birds to build wider nest cups, thereby reducing crowding of the young without paying the costs of increased exposure to severe climatic effects. Although it was not quite significant, island birds also built nests with a shallower internal depth, perhaps also suggesting the greater depths of continental species may be an adaptation to reduce exposure.

Island birds generally built nests with larger external nest depths but shallower internal nest depths, indicating that they may build a thicker bottom (floor) than their continental relatives. Hoi et al. (1994) suggested that bottom layer thickness was important for nesting success in penduline tits (*Remiz pendulinus*), with females selecting mates based on the quality of nests that they build (Hoi et al. 1994). Large nests in this species act a cue for nest quality with resulting higher fledging success associated with larger nests and thicker nest floors. The role of mate choice in nest size in the species I studied is unknown. Continental birds may invest less in the thickness of their nests due to higher levels of predation. Slagsvold (1989*b*) reported that open-nesters (which have higher predation levels) have shallower nests than hole-nesting birds, suggesting that internal cup depth may be limited by predation rates as nests need to be shallow enough for parents to have unobstructed views of their surroundings. It may also be that internal cup depth is also affected by nestling begging activities (vocalisations, stretching, gaping and pushing for food) as begging can often attract predators to the nest (Haskell 1994). Deeper internal cups may obstruct a predator's awareness of the nestling's begging activities and reduce predation rates. However, this remains to be tested. Insular birds showing trends towards building thicker nest floors may just be an adaptation to increase nest quality, whereas continental birds experiencing higher predation rates may construct nests to reduce the nest conspicuousness to their predators.

Domed nests of continental species did not significantly in size from island domed-nesting species; however, the results were limited by small sample sizes and did not include internal dimensions. Studies on predation rates (Ricklefs 1969; Hoi and Winkler 1994) suggest that domed-nesting species have lower predation rates, probably due to more concealment and protection. Given this difference it is surprising that passerines families are more frequently cup builders (60%) than dome builders (38%; Collias 1997). Perhaps there may be an advantage to shape of the nest, with rarer domed nests protected from predators with a search image for the more common cup nests. Birds that build cup nests in contrast, are more exposed to predators and less effective in conserving heat (Nilsson 1986). Clearly, further work is needed to determine the costs and benefits of domed nests over cup nests and whether this varies between island and continental species.

The continental island birds differed in nest dimensions from their continental relatives, showing an increase in the width of the cup sizes and overall increase in nest size. New Zealand and New Caledonia, like many oceanic islands elsewhere, have a depauperate mammal fauna and are as isolated as many true oceanic islands. The distinction between continental islands and oceanic islands stems from the disproportionate number of continental lineages found on these continental islands, a result of once being connected to the supercontinent Gondwana (Daugherty et al. 1993). Birds may have once coexisted with large predators on these continental islands, Recent studies have suggested that mammals were present in New Zealand during the Cretaceous period (Pole 1994; Worthy et al. 2006). This indicates that mammals may only have disappeared from New Zealand in the Middle Miocene (a few million years ago) due to climatic cooling, which is much later than the presumed 82 million years previously thought (Worthy et al. 2006). Regardless of the date of actual mammalian extinction, the

differences in the predator fauna of these continental islands and a true continent suggests that predation has played a key role in the evolution of nest size. The continental islands had a variety of avian predators but these likely had a smaller impact on nest success, with nocturnal predators (laughing owl *Sceloglaux albifacies*; New Zealand owlet-nightjar *Aegotheles novaezelandiae*; New Caledonian owlet-nightjar *Aegotheles savesi*) feeding primarily on invertebrates, frogs or lizards, and with diurnal predators such as the New Zealand goshawk (*Circus eylesi*) or the New Caledonian sparrowhawk (*Accipiter haplochrous)* feeding primarily on birds in flight (Holdaway 1989). This contrasts with the high nest predation faced by these islands today. Introduced species account for 55% of the nestling losses in the endemic New Caledonian Kagu (*Rhynochetos jubatus*; Ekstrom et al. 2002) and 61% over 13 species of New Zealand birds (Innes et al. 2010). As continental island birds once coexisted with these predators, it may be that length of isolation from predators of bird nests is the biggest factor influencing the sizes of nests.

Studies show that the structure and size of bird nests are affected by many variables such as phylogeny (Møller 1989), sexual selection (Hoi et al. 1994) and number of builders (Soler et al. 1998). I investigated three factors (body size, clutch size and latitude) that may have exerted a strong effect on nest size. Body size exerted strong effects on nest size. This is not surprising given that internal cups are often moulded to the size of the incubating parent (Collias 1986). Theories on body size suggest that island species tend to conform to a medium body size or the 'island rule' (Lomolino 2005). Fluen (2008) suggested that such theories may often be misplaced (all island birds being larger bodied) given that research on island bird body size focuses on small bodied passerines, which conform to the 'island rule' and increase in body size. Body size in my two comparisons however, did not differ between the island and continental groups. However, in both

comparisons the island birds averaged slightly smaller than the continental birds suggesting that nest size differences, (when body size is controlled for in an analysis) may be even larger than what was found in this study. Clutch size is another factor that significantly affected nest dimensions. Birds with large clutch sizes may build larger nests to reduce overcrowding. Nest predation being both an ultimate and proximate factor effecting clutch size may also indirectly select for smaller nest sizes (Møller 1990). Clutch sizes differed among my treatments with insular birds laying smaller clutches and than their continental relatives. Furthermore nest size should be affected by latitude with temperate birds likely building larger nests to accommodate lower temperatures. This is supported by Kern and Van Riper (1984) who showed that the common amikihi (*Hemignathus v. virens*) vary their nests in size and architecture (to increase incubation potential) depending on altitudinal locations. Latitude however was not significant in my analysis, probably due to the largely temperature and tropical environments in which I gathered data from the literature (i.e., few data were available from polar and alpine regions). Given that all three life-history traits exerted some effects on nest size it is realistic to expect that differences between the two groups influenced differences in nest sizes between island and continental species. Island clutch sizes (smaller) and latitude (more tropical) might be expected to negatively influence the size of nests of island birds, although this does not appear to be the case. To fully understand how factors such as clutch size and latitude affect nest sizes in island birds a larger sample would be needed in which such potentially confounding effects could be controlled statistically.

These results suggest a number of selective pressures shaping the construction of insular bird nests. However, research around the structure and size of nests is lacking. Future studies could investigate possible differences between island and continental bird

nests in terms of the composition of their nests. The density of nests may be the most influential factor determining incubational quality of nests (Skowron and Kern 1980). It would be interesting to compare nest densities between island and continental birds to examine whether island birds (less limited by the size of their nests) build thicker but lighter nests compared to continental birds which may make thinner, denser nests (smaller nest size). Further research could include island species with populations facing different predation histories (populations with no predators present and populations with predators present). Results from this may show how birds are responding to high predation pressures (i.e., whether they are reducing the nest size since the arrival of introduced predators).

My findings show in general, that insular birds build larger nests than their continental relatives. I found a tendency for island birds to build larger external dimensions (possibly to increase incubation potential) and even larger internal diameters (less overcrowding of young) indicating that insular nests are likely built to maximise reproductive success in the nest. Continental birds in contrast, build nests that are smaller with deeper internal depths as birds evolving on continents are faced with much higher rates of nest predation. Nest predation can have a severe impact on reproductive success and may select for smaller clutch sizes (Lima 1987) and nest sizes (Møller 1990). This size disparity is significant in that it further highlights the risk that insular birds face with the current wave of predators that have been introduced to islands. Introduced predators are accountable for about half of all island bird extinctions with cats and rats the most notorious killers (Courchamp et al. 2003). The larger nests of insular birds may make the nests more accessible to predators (both visually and olfactory) compared to similar continental species. The large number of insular birds that have become extinct or are now critically threatened may have partially arisen from their larger nests. Given the current

status and bird populations conservation management directed at nests may be vital for the long term success of island birds.

4.6 References

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Table 4.1. Average life-history traits of the cup and domed nest building island and continental species with the standard deviations shown. Ranges and sample sizes (number of species) are given in parentheses.

	Life-history traits		
Species	**Body size (g)**	**Clutch size**	**Latitude (°)**
All nests			
Island	44.0 ± 95.7	2.5 ± 0.9	15.0 ± 11.1
	(6-520, 34)	(1-4, 32)	(0-36, 34)
Continental	60.1 ± 173.3	3.3 ± 1.1	25.6 ± 13.9
	(5-967, 34)	(2-5, 34)	(0-54, 34)
Cup nests			
Island	51.9 ± 106.4	2.4 ± 0.8	17.1 ± 11.1
	(6-520, 27)	(1-4, 26)	(0-36, 27)
Continental	72.0 ± 193.4	3.3 ± 1.1	28.4 ± 12.9
	(5-967, 27)	(2-5, 27)	(4-54, 27)
Domed nests			
Island	13.9 ± 5.1	3.3 ± 1.1	6.7 ± 6.8
	(9-24, 7)	(2-4, 6)	(0-16, 7)
Continental	13.5 ± 3.4	2.9 ± 0.9	14.9 ± 13.4
	(8-19, 7)	(2-4, 7)	(0-39, 7)

Table 4.2. Average life-history traits for paired 'continental' island and Australian species with standard deviations shown. Ranges and sample sizes (number of species) are given in parentheses.

	Life-history traits		
Species	**Body size (g)**	**Clutch Size**	**Latitude**
"Continental" island	16.3 ± 7.1	2.9 ± 0.9	36.0 ± 9.6
	(8-27, 7)	(1-4, 7)	(22-44, 7)
Australian	17.2 ± 7.4	2.7 ± 0.4	32.3 ± 5.1
	(7-27, 7)	(2-3, 7)	(23-36, 7)

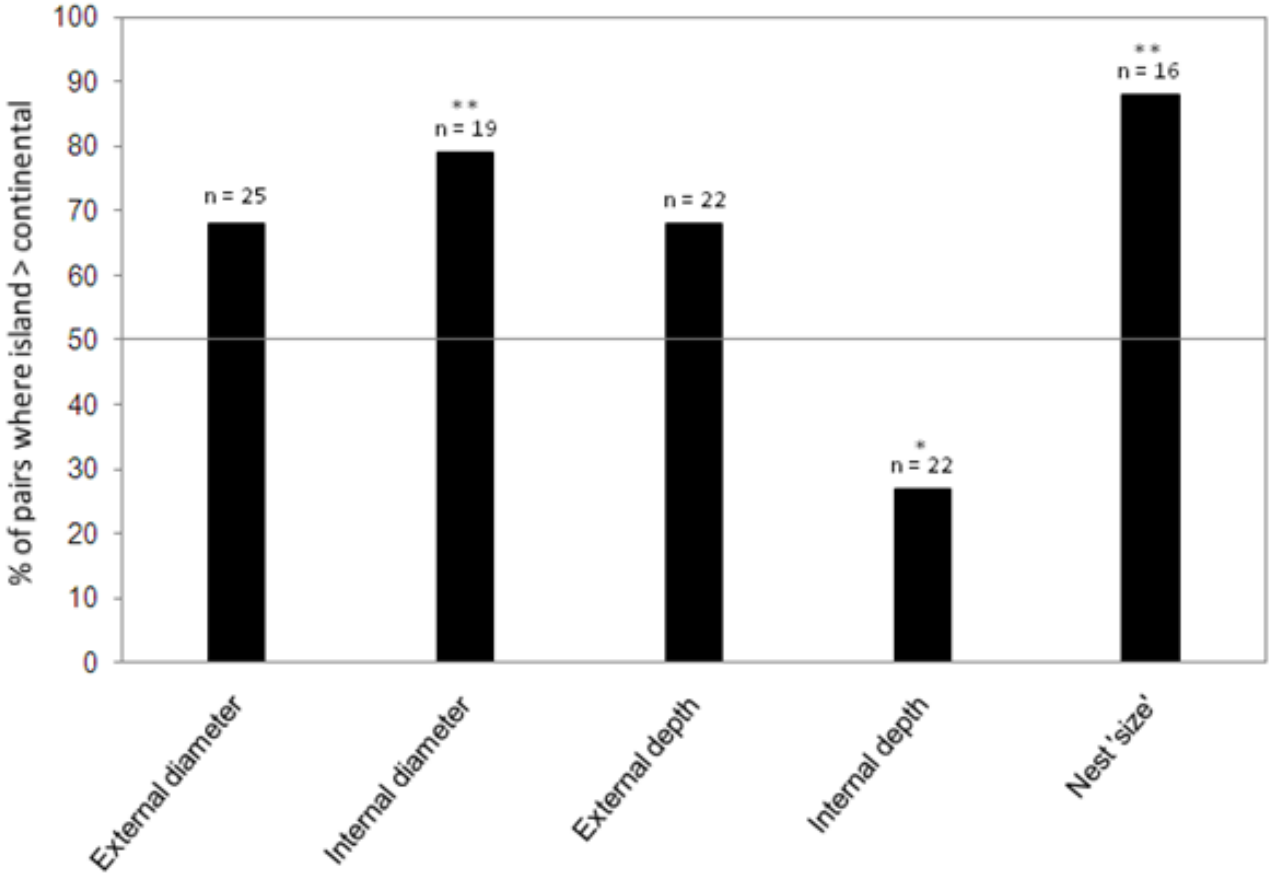

Figure 4.1. Graph showing the percentage of cup building species pairs in which the island species were larger than continental species in the specified nest dimension. (Nest 'size' was an estimate using the four individual dimensions for cupped nests and the two external nest measurements for domed nests; as explained in the methods section). The line at 50% represents the percentage pairs expected to show an increase by chance; the null hypothesis. (* = $p \leq 0.1$, ** = $p \leq 0.05$).

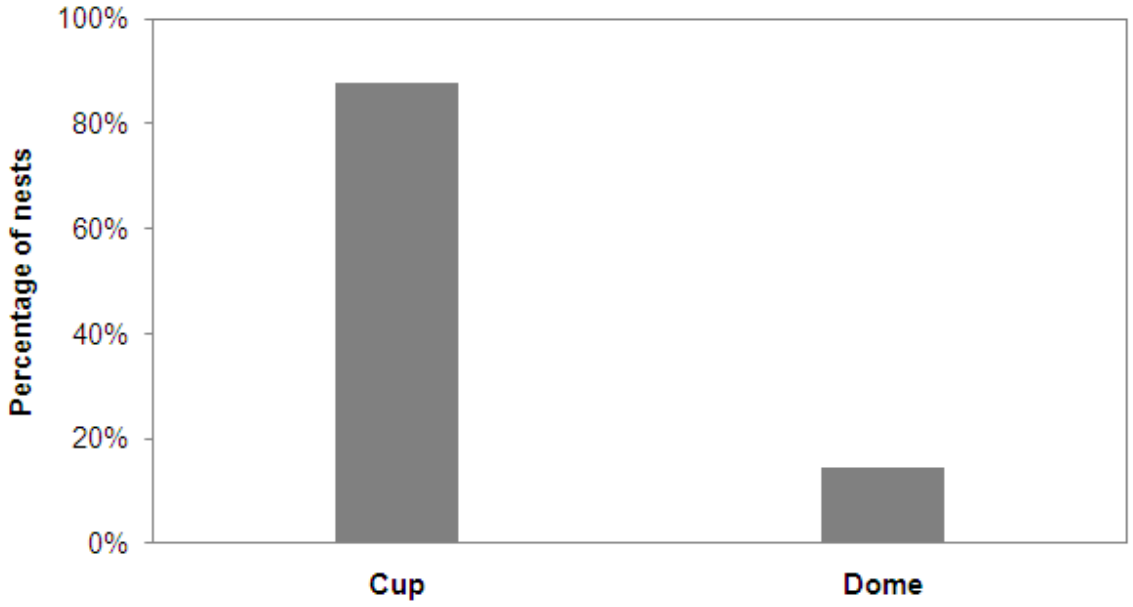

Figure 4.2. Graph showing the difference in the percentage of island species pairs which showed an increase in nest 'size' relative to their continental counterparts.

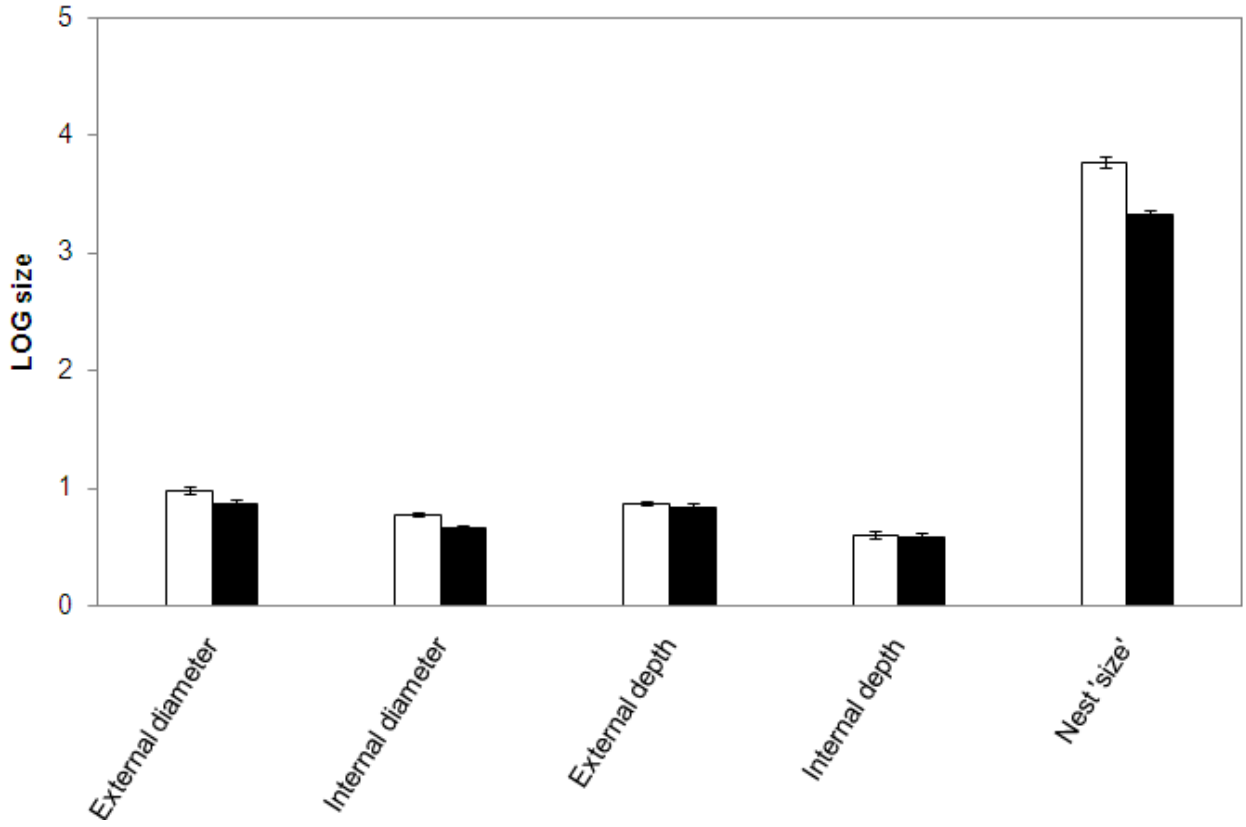

Figure 4.3. Graph showing the LOG (base 10) dimension sizes of all the continental 'island' (open bars) and Australian species pairs (black bars) used in this study. Standard errors are shown.

Chapter 5

5.1 General Discussion

The last three chapters have revealed some interesting differences between insular and continental birds. These differences are likely the result of different selective pressures that have acted upon insular species and have resulted in the evolution of different life-histories compared to continental species. The avifauna of New Zealand and other small isolated islands are unique in a number of ways, but at the same time share characteristics that reflect the insular environment, especially in a variety of reproductive traits in and around the nest. My study of the unique characteristics of insular birds, such as their increased odour, has also revealed the vulnerability of insular birds to introduced predators and highlights the need to consider life history evolution in the conservation of insular species.

Initially, I suggested that differences in the evolutionary history of island and continental species may cause insular birds (New Zealand birds in this case) to sustain higher levels of predation on artificial nests due to increased volatility of their preen waxes that make their nests more conspicuous to predators that use olfaction to locate their prey. I found that indeed there were differences in the predation rates with the risk of depredation significantly higher among the nests baited with the preen waxes of endemic species compared to the nests baited with wax from continental species or control nests with no preen wax. At the species level, endemic species were also significantly depredated more frequently than continental species. These observations support the hypothesis that island

birds have evolved more volatile preens waxes due to lack of selective pressure from predatory mammals.

Although New Zealand is large and similar to continents in many ecosystem attributes, until humans arrived, the predation regime was significantly different to that of continents. In contrast to continental areas, the avifauna of New Zealand evolved in the absence of predatory olfactory-searching mammals for millions of years, and this likely meant that the selective pressures from the native predators (mostly birds) would not have shaped preen wax volatility as is found in continental birds. It is likely that the isolation of islands from mammalian predators and other selective pressures have resulted in an absence of seasonal preen wax changes for the majority insular birds. Island birds may use preen waxes for various functions other than olfactory crypsis and may often increase in the volatility of the waxes. As one-fifth of the world's bird species are restricted to islands (Johnson and Stattersfield 1990) and with recently introduced mammalian predators now ubiquitous on islands (now exert influences on 80% of all islands; Howald et al. 2007), this represents a significant proportion of bird species that will highly vulnerable to nest depredation from mammalian predators.

Chapter 3 examined differences in nesting behaviour between insular and continental birds. Islands are isolated, and animals on islands experience only a subset of the selective predation pressures faced by continental species. Thus, the absence of some key types of predators could lead to a loss of anti-predator behaviour, and life-history strategies may also shift towards a strategy that involves more parental-investment (Blumstein 2002). I performed flushing experiments on endemic New Zealand and continental birds to assess if there is indeed a lack of anti-predatory behaviours in island birds. As expected, I found that New Zealand birds were much less likely to flush upon my

approach (a potential predator) at the nest. Endemic birds also flushed later from the nest when I approached, returned to the nest sooner after flushing, and did not reduce their activity around the nest after being flushed (i.e., showed higher level of parental investment). Predation risk is thought to play an important role in shaping of life history strategies of birds (Ricklefs 1969; Lima 1987). Birds are expected to behave in ways that reduce their overall risk of predation (Eggers et al. 2005; Fontaine and Martin 2006; Eggers et al. 2008), yet many species of insular birds display many behaviours that appear maladaptive towards predators including naivety (Lowman 2005) and reduced flocking (Beauchamp 2004). The flushing behaviour of endemic New Zealand birds at first glance also appears maladaptive, as were a real predator to approach a nest in the manner I did, it is easy to imagine that the risk of being preyed upon would be greater than that experienced by the continental species that readily flushed. However, before human arrival, endemic New Zealand birds evolved with avian predators. Flushing from nests when such predators approached would likely be costly as avian predators that search with visual cues when hunting might be able to more easily detect and predate a flying bird than one sitting unnoticed on the nest. Instead, remaining cryptic and still on the nest may increase the chances of survival. The result is changes in many behavioural traits around the nest, which function in increasing the survival of their offspring. Currently however, the introduction of mammalian predators makes these nesting behaviours maladaptive, highlighting the risk for threatened insular birds.

My fourth chapter investigated the patterns of nest size between insular passerines and their continental relatives. Nest building behaviour and construction are determined largely by genetics although many other environmental factors also can influence the overall nest structure (Møller 1989). The evolution of nest structure and size may involve

trade-offs between the benefits and costs of building a nest including nest sizes and their conspicuousness to predators (Møller 1990), and between energy expenditure and predation risk during nest building (Soler et al. 1998). Specifically, in this chapter I compared changes in nest size dimensions of insular birds and their continental relatives on a number of island groups around the world. I found that the nests of island birds were significantly larger and were often characterised by having larger internal nest diameters and overall nest 'sizes'. Nest size increases were found for both small oceanic islands all around the world and the continental 'islands' (landmasses formerly connected to continents) that lacked native mammalian predator faunas. This ultimately suggests that predation risk may be one of the key selective pressures regulating nest size in birds. Nest predation exerts large influences on the reproductive success of birds (Møller 1990; Sanders and Maloney 2002). Island species, may be less limited by the effects of predation compared to the effects of intraspecific competition. Thus, island birds might be under stronger selection to build larger nests to increase the survival of their young. The benefits of a larger nest derive from reduced overcrowding of young in the nest, greater stability (Slagsvold 1982), and increased incubation efficiency (Skowron and Kern 1980). Continental birds that build smaller nests may invest less energy per offspring (large clutches with smaller nests) but construct nests to reduce predation rates. The disadvantage of the larger nests of insular birds it that this may make the nests more conspicuous and accessible to predators compared to similar continental species. However, this risk may have been small in the original predator-poor environments in which insular birds evolved. With exotic predators introduced on islands all around the world, the large nests of insular birds may now be a liability and be increasing their vulnerability to predation.

Altogether my 3 data chapters illustrate interesting changes that have occurred in the evolution of insular birds. The increased risk of predation due to their preen waxes, the lack of anti-predatory escape behaviours and the larger nests sizes indicate that island environments select for quite different strategies of reproduction. Island nesting birds seem to invest more into the success of their young compared to continental birds. Island species are generally 'K' selected with traits including longer life expectancies, and the production of fewer offspring that require extensive parental care until they mature (MacArthur and Wilson 1967). K-selection on islands may result from relatively higher stabilities, high intraspecific competition and low predation risks. Species on island environments would likely succeed if they reduced energy input into costly non-reproductive activities. Anti-predatory behaviours (Blumstein et al. 2006) and changes in preen wax volatilities (Reneerkens et al. 2006) are known to be costly energetic traits. Island species may have reduced their anti-predatory defences and instead invested in other aspects of their life-histories. These changes are widespread in island birds with the extreme being the evolution of flightlessness found in some island rails. This is presumably an adaptation for increased energy conservation reducing energy expenditure in island environments prone to resource limitation (Mcnab 1994). Island environmental differences and the long arduous process of evolution therefore seem to constrain the island avifaunas and their nesting ecology to build larger, smellier nests with reduced anti-predatory behaviours.

Additionally my study indicates there is much further research possible on the evolution of insular avifaunas. Island environments affect the evolution of many different facets of avian life-histories and there are more opportunities to tease out the differences from continental birds in life-history attributes. My study focused predominantly on changes in New Zealand birds life-histories. However, New Zealand's islands are different

to the majority of other islands globally in that they are large and 'mainland like.' Large studies involving various island environments (different in size, isolation, species diversity, predator risk, human colonisation etc.) will help identify the different factors that shape insular species life-histories. Specifically, further analyses on preen waxes from nesting birds from a range of islands to assess the "smelliness" of the nest to predators will provide more information on the variation in the volatility of preen waxes of island birds and how this affects their risk of predation. Further behavioural investigations into anti-predatory behaviours at the nest would help in assessing the plasticity of behavioural traits in insular birds. Different behavioural traits may have varying degrees of plasticity, and different periods by which a trait undergoes functional adaptations. Research into nesting behaviours of island birds could examine behavioural differences between islands with varying degrees of human impact. This could be useful for understanding changes in plastic traits that have occurred since predators were introduced and provide valuable insights into the future of conservation (i.e., should we continue advocating complete predator removal or reduce predator numbers to a sufficient state that allow important anti-predator behaviours to evolve). An expansion on island nest design (including interactions between the size, shape and materials used in nests) differences between the island and continental avifaunal groups will help generate more knowledge in the attributes that contribute to conspicuousness at nests (Massaro et al. 2008). Furthermore, there may be synergistic interactions between nesting traits that will exacerbate the vulnerability of island nests to predators. One could look at different nesting traits of island species and investigate whether that increases in certain traits exacerbates the effects of other traits. Larger nest sizes for example, may in turn increase the olfactory volatility retained in the nest making the nest both visually and olfactory more conspicuous to predators.

We need a detailed understanding of all facets of insular bird's life-histories to understand how and why they are different from continental relatives. This will provide the insight conservationists need to identify the key attributes that make island species so vulnerable to introduced predators. As we identify and understand more of the evolutionary history of insular birds and their differences, we then can fully evaluate the best solutions to their current threatened status. We may even be able to prevent any more species of insular birds succumbing to this global, human induced extinction event.

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Appendix 1. List of species pairs used in chapter 4 including the region in which each member of the pair evolved. The first species in each pair is the "island" species and the second species in the "continental" species.

Pair #	Species	Region
1	*Fringilla teydea*	Canary Islands
	Fringilla coelebs	Europe
2	*Serinus canaria*	Canary Islands
	Serinus citrinella	Europe
3	*Saxicola dacotiae*	Canary Islands
	Saxicola torquatus	Europe, Africa
4	*Zosterops conspicillatus*	Guam
	Zosterops luteus	Australia
5	*Zosterops modesta*	Seychelles
	Zosterops pallidus	South Africa
6	*Speirops leucophaeus*	Príncipe
	Zosterops senegalensis	Africa
7	*Tersiphone atrochalybeia*	São Tomé
	Tersiphone rufocinera	South Africa
8	*Turdus olivaceofuscus*	São Tomé
	Turdus olivaceus	South Africa
9	*Turdus poliocephalus*	Christmas Island
	Turdus philomelos	Europe, Asia
10	*Mimus graysoni*	Socorro Island
	Mimus saturninus	South America
11	*Acrocephalus taiti*	Henderson Island
	Acrocephalus orientalis	Asia

12	*Acrocephalus sechellensis*	Seychelles
	Acrocephalus gracilirostris	Africa
13	*Myzomela rubratra*	Chuuk
	Myzomela sanguinolenta	Australia
14	*Vireo caribaeus*	San Andrés Island
	Vireo griseus	United States of America, Mexico
15	*Vireo gracilirostris*	Fernando de Noronha Islands
	Vireo olivaceus	North America
16	*Nesotriccus ridgwayi*	Cocos Islands
	Serpophaga griseiceps	Argentina
17	*Vermivora celata sordida*	Channel Islands (North America)
	Vermivora celata lutescens	North America
18	*Melospiza melodia micronyx*	San Miguel Island
	Melospiza melodia heermanni	United States of America
19	*Aphelocoma insularis*	Santa Cruz Island
	Aphelocoma californica	Mexico
20	*Corvus hawaiiensis*	Hawaii
	Corvus corax	North America
21	*Corvus kubaryi*	Guam
	Corvus bennetti	Australia
22	*Pomarea dimidiata*	Cook Islands
	Monarcha melanopsis	Australia
23	*Rhipidura rufifrons uraniae*	Guam
	Rhipidura rufifrons intermedia	Australia
24	*Rhipidura verreauxi*	Fiji
	Rhipidura phasiana	Australia

25	*Contopus oberi*	St. Lucia
	Contopus pertinax	Mexico
26	*Amphispiza belli clementeae*	San Clemente Island
	Amphispiza belli belli	California
27	*Myiagra freycineti*	Guam
	Myiagra rubecula	Australia
28	*Erythrura trichroa clara*	Chuuk islands
	Erythrura trichroa macgillovrayri	Australia
29	*Prinia molleri*	São Tomé
	Prinia bairdii	Africa
30	*Chalcomitra balfouri*	Socotra
	Chalcomitra amethystina	South Africa
31	*Anabathmis hartlaubii*	Príncipe
	Anthreptes rectirostris	Africa
32	*Foudia eminentissima*	Comoros
	Euplectes ardens	South Africa
33	*Geospiza fuliginosa*	Galapagos Islands
	Coereba flaveola	Panama
34	*Passer iagonesis*	Cape Verde Islands
	Passer domesticus	Europe
35	*Mohoua novaseelandiae*	New Zealand
	Falcunculus frontatus	Australia
36	*Rhipidura fuliginosa*	New Zealand
	Rhipidura albiscapa	Australia
37	*Megalurus punctatus*	New Zealand
	Megalurus timoriensis	Australia

38	*Petroica macrocephala*	New Zealand
	Petroica multicolour	Australia
39	*Anthornis melanura*	New Zealand
	Certhionyx variegatus	Australia
40	*Zosterops lateralis griseonota*	New Caledonia
	Zosterops lateralis lateralis	Australia
41	*Phylidonyris undulatus*	New Caledonia
	Phylidonyris albifrons	Australia